COOPERATION AND COMPETITION IN KIN ASSOCIATIONS

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COOPERATION AND COMPETITION IN KIN ASSOCIATIONS

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The presence of nearby kin, kin-directed cooperation across territory boundaries, and kin competition over extra-pair matings are potentially important influences on social evolution, yet our understanding of the complex relationships among these factors is incomplete. For example, the costs of kin competition can theoretically select for dispersal, yet other theory suggests that kin-selected reductions in the intensity of competition may counteract these costs and allow individuals to reap other benefits of kin-based living. Using both theoretical and empirical approaches, I investigate how kin structure and extra-pair mating affect each other as well as cooperative behavior. In the first chapter, I investigate competition between unrelated males over extra-pair paternity, deriving the conditions under which females are selected to invest in conflict and suggesting that males may maximize their fitness by associating in "hidden leks." In the second chapter, I show how genetic mating system and kin structure can affect the relative costs and benefits of helping versus independent breeding, suggesting that kin structure may in fact increase the benefits of breeding independently relative to rearing younger siblings. In the third chapter, I examine the effects of relatedness on extra-pair mating competition, and the effects of this kin competition on the costs and benefits of philopatry. I demonstrate that the reduced optimal investments in competition among kin mean that males benefit from philopatry, even in the face of paternity loss, and that paternity gains are skewed towards the relative with higher heritable genetic quality. In the fourth chapter, I experimentally investigate the cryptic

cooperative behaviors that are expressed in western bluebird (*Sialia mexicana*) kin neighborhoods. I find that, while first-order male relatives exhibit cross-territorial assistance responses in dire situations, these responses are less frequent than those by stay-at-home helpers. In the fifth chapter, I examine the effects of kin presence on western bluebird extra-pair mating, and suggest that patterns resulting from kin-based living, such as paternity buffering, may influence the population genetic mating system. Together, these results indicate that the complex, and often cryptic, cooperative and competitive interactions that occur among independently breeding relatives in kin neighborhoods can importantly affect social evolution.

BIOGRAPHICAL SKETCH

Caitlin Alice Stern was born in Juneau, Alaska on 1 October, 1984. Caitlin grew up in Haines, Alaska, where she developed an early interest in biology during many outdoor expeditions with her parents. At thirteen, Caitlin began volunteering for a Wildlife Conservation Society (WCS) study of the resident bald eagle population in Haines, staying with the project for three years and winning awards for her research including the Young Naturalist Award from the American Museum of Natural History and a semifinalist place in the Intel Science Talent Search. After an internship at the WCS headquarters in New York City, Caitlin was hired as a field assistant on a different WCS project, studying ponderosa pine forest songbirds in northern California. Caitlin entered Harvard University in 2001, concentrating in biology. Caitlin completed two more field seasons with WCS before moving to Isle Royale National Park for her senior thesis research, which focused on the behavioral rules used by foraging moose and sharpened Caitlin's interest in the feedbacks between ecological factors and behavior. During her senior spring, Caitlin developed a strong interest in the evolution of cooperative breeding behavior, which led her to apply for an internship with Janis Dickinson's western bluebird study at Hastings Reservation in Carmel Valley, California, a position that she began one week after graduating from Harvard with honors in biology in 2005. Caitlin spent the next year at Hastings, leading the spring field crew. Caitlin began her PhD research in 2006 in the Department of Neurobiology and Behavior at Cornell University, returning to Hastings yearly to work with the western bluebird population. Having completed her graduate work, Caitlin will move to a postdoctoral research position at the University of North Carolina at Chapel Hill, where she will pursue her interest in mathematically modeling the evolution of social behavior.

To my parents, Mark Sogge and Cecily Stern, who have supported me in every endeavor

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CHAPTER 1

CLUSTERING NEAR A HIGH-QUALITY MALE DECREASES PATERNITY LOSS THROUGH DILUTION EFFECTS

Caitlin A. Stern and H. Kern Reeve

SUMMARY

Mating outside the pair bond is widespread across socially monogamous species with biparental care (Petrie and Kempenaers 1998; Griffith, Owens, and Thuman 2002; Westneat and Stewart 2003). Extra-pair mating is often associated with mate guarding (Birkhead and Møller 1992), a behavior which is rarely exhibited by females exhibit (Creighton 2000) despite possible advantages (Petrie 1992; Petrie and Hunter 1993) and frequently, but often ineffectively exhibited by males (Kempenaers, Verheyen, and Dhondt 1995; Johnsen, Lifjeld, and Rohde 1998; Chuang-Dobbs, Webster, and Holmes 2001; Marthinsen et al. 2005). Because the average percentage of extra-pair offspring in a brood is the result of interactions among at least two mated pairs, evolutionary game theory (Maynard Smith 1978) approaches may help explain patterns of behavioral investment in conflict (e.g., mate guarding) and the resulting rates of EPP. Here we show that an *n*-pair tug-of-war model, in which all individuals' decisions are allowed to evolve simultaneously, both explains the widely-observed absence of mate guarding by females and predicts average EPP rates strikingly close to those measured empirically. We found that females may be selected to invest in conflict over energy allocated to paternal care, but only invest in conflict over the success of extra-pair copulation attempts under restricted conditions. Further, we found that the predicted average EPP rate, ranging from 12.3% to 18.6%, is highest

when few pairs interact directly. Per brood EPP decreases with the number of interacting pairs, suggesting that low-quality males could minimize paternity loss by clustering near a high-quality rival.

INTRODUCTION

When breeding territories are spatially clustered, populations of socially monogamous birds may contain "hidden leks" analogous to the aggregation of males on traditional leks (Wagner 1997). Non-preferred males may breed near a preferred male, benefiting the preferred male by creating additional extra-pair mating opportunities and decreasing his paternity loss ("paternity buffering") as well as increasing non-preferred male fitness through e.g. increased pairing success (Greene et al. 2000). Evidence for this pattern comes from semi-colonial species such as purple martins (*Progne subnis*) (Wagner 1997) and Bullock's orioles (*Icterus bullockii*) (Richardson and Burke 1999) as well as from non-colonial species such as lazuli buntings (*Passerina amoena*) (Greene et al. 2000).

The model we present here suggests that non-preferred males breeding near a preferred male may also increase their fitness by distributing the preferred male's extra-pair mating effort across a greater number of potential extra-pair females, an idea we term the hot-not hypothesis (cf. the hotspot (Bradbury and Gibson 1983) and hotshot (Beehler and Foster 1988) hypotheses). This diminished risk of paternity loss is analogous to "dilution effects," in which an individual minimizes its own risk of attack from a predator by associating with other potential prey (Foster and Treherne 1981).

A dichotomy between preferred and non-preferred males may arise when females select extra-pair mates on the basis of assessable characteristics that indicate heritable genetic quality. Both empirical and theoretical studies suggest that male age may be one such characteristic (Kokko and Lindstrom 1996; Kokko 1998; Brooks and Kemp 2001; Green, Peters, and Cockburn 2002; Tarof et al. 2012). Although other bases of female choice likely exist (Fromhage, Kokko, and Reid 2009), we focus here on the situation in which a female accepts an extra-pair mate on the basis of his "breeding value for total fitness" (Hunt et al. 2004), which we term "quality" for brevity.

Framing conflicts mathematically is especially useful when verbal arguments make opposing predictions. A major question in the current literature is whether increasing the number of effectively interacting pairs – either through breeding synchrony (Birkhead and Biggins 1987; Stutchbury and Morton 1995) or breeding density (Morton, Forman, and Braun 1990) – will increase or decrease the average percentage of offspring in a brood sired by an extra-pair male (extra-pair paternity, EPP), since both patterns seem logically justified and have empirical support (Neodorf 2004). Here we examine the situation in which a high-quality pair interacts with n other, lower-quality pairs, with all n pairs having equal quality, for a total of $n + 1$ pairs. We assume that pairs are formed through positive assortative mating on quality (Norris 1990; Norris 1993; Härdling and Kokko 2005). We also assume that females mated to high-quality males will not accept extra-pair copulations, while females mated to lower-quality males may do so. Across species, approximately 60% of males than gain EPP do not lose within-pair paternity (Table 1.1), corresponding to our high-quality males. Of the other three categories of males possible – males that 1) gain EPP and lose within-pair paternity (WPP), 2) lose WPP but gain no

EPP, and 3) neither gain EPP nor lose WPP – our model captures one: males that lose WPP but gain no EPP, corresponding to our low-quality males. Incorporating the other possible male categories represents an important future extension of this model. The model builds upon previous game theoretic models of conflict over paternity (Fishman, Stone, and Lotem 2003; Kokko and Morrell 2005) by both incorporating conservation of paternity (Houston and McNamara 2002), meaning that any paternity lost by one male must be gained by another, and simultaneously solving for the optimal allocation among different decisions, thus capturing the tradeoffs individuals face due to limited time and energy to invest in conflict.

METHODS

The two conflict types in this model, *allocation conflict* and *interference conflict*, correspond to within-pair conflict over investment in parental care, and conflict over the success of EPC attempts, respectively (Figure 1). Investment in allocation conflict includes behaviors that impede a mate's ability to seek EPCs rather than provide parental care, such as interrupting EPC advertisement calls. Investment in interference conflict includes behaviors that decrease a mate's EPC success, such as interrupting copulations (Tarof and Ratcliffe 2000).

Table 1.1 The percentage of males that both gained extra-pair and lost within-pair paternity in a subset of species for which such data are available. Across all eight studies, an average of 41% of the males that gained extra-pair paternity also lost within-pair paternity. All families listed belong to the order Passeriformes.

Family	**Species**	**% broods with EPY**	**% young that are EPY**	**% males that both gained and lost paternity, out of all males that gained EPP**	**Source**
Rhipiduridae	*Rhipidura albiscapa*	64 (16/25)	55 (27/49)	100 (3/3)	(Hoffman et al. 2010)
Tyrannidae	*Tyrannus tyrannus*	61 (54/89)	47 (124/257)	56 (15/27)	(Dolan et al. 2007)
Parulidae	*Dendroica petechia*	54 (70/130)	33 (160/484)	45 (9/20)	(Yezerinac and Weatherhead 1997)
Parulidae	*Wilsonia citrina*	35 (42/119)	27 (95/356)	29 (4/14)	(Stutchbury et al. 1997)
Emberizidae	*Junco hyemalis*	34 (13/38)	28 (53/187)	33 (3/9)	(Ketterson et al. 1998)
Muscicapidae	*Ficedula hypoleuca*	20 (106/533)	40 (45/113)	32 (8/25)	(Canal, Potti, and Dávila 2011)
Paridae	*Parus major*	40 (31/78)	9 (58/681)	29 (5/17)	(Strohbach et al. 1994)
Fringillidae	*Carpodacus erythrinus*	34 (21/62)	18 (48/266)	0 (0/9)	(Albrecht et al. 2007)

We began by including all possible investments in conflict (Figure 1a) in the fitness functions for Male 1 (M1), Female 1 (F1), Male *i* (the *i*th of *n* other males; M*i*), and Female *i* (the *i*th of *n* other females; F*i*). Using a tug-of-war approach, wherein the fraction of contested resource an individual obtains is proportional to the individual's investment divided by the sum of all investments in conflict (Reeve, Emlen, and Keller 1998), and assuming that each individual's starting energy budget is equal to 1, we define the fraction of M1's energy that he invests in seeking EPCs (i.e., the result of allocation conflict between M1 and F1) as

$$m_1 e = \left(\frac{x_1}{x_1 + y_1}\right) * (1 - x_1) \tag{1}$$

Where x_1 is M1's investment in increasing the fraction of energy he invests in seeking EPCs relative to the fraction he invests in parental care, and y_1 is F1's investment in resisting his effort to do so. By similar logic, the fraction of F*i*'s energy that she invests in seeking EPCs (i.e., the result of allocation conflict between F*i* and M*i*), is

$$f_i e = \left(\frac{x_i}{x_i + y_i}\right) * (1 - x_i) \tag{2}$$

The energy available after the allocation conflict is invested in the interference conflict over the success of M1's and F*i*'s EPC attempts, with F1 and M*i* contributing interference efforts z_1 and z_i, respectively. Both M1's and F1's investments in interference conflict are distributed over the *n* other pairs with which they interact. Thus, the percentage of offspring M1 sires in the *i*th brood is

$$epp = \frac{\left(\frac{m_1 e}{n}\right) + f_i e}{\left(\frac{m_1 e}{n}\right) + f_i e + \left(\frac{z_1}{n}\right) + z_i} \tag{3}$$

To incorporate the relative qualities of the pairs, we assumed a simple additive effect with each parent contributing half of the offspring's quality value such that the quality of offspring produced by, e.g., M1 and Fi, is equal to $q_{m1} + q_{fi}$. Using these terms along with those previously defined, we formulate the fitness functions for all individuals involved in the conflict:

$$w_{m1} = \left[n * epp * \left(\left(\frac{y_i}{x_i + y_i} \right) * (1 - x_i) + (1 - y_i - z_i) \right) * \left(q_{m1} + q_{fi} \right) \right] + \left[\left(\left(\frac{y_1}{x_1 + y_1} \right) * (1 - x_1) + (1 - y_1 - z_1) \right) * (q_{m1} + q_{f1}) \right] \quad (4)$$

$$w_{f1} = \left[\left(\left(\frac{y_1}{x_1 + y_1} \right) * (1 - x_1) + (1 - y_1 - z_1) \right) * (q_{m1} + q_{f1}) \right] \quad (5)$$

$$w_{mi} = \left[(1 - epp) * \left(\left(\frac{y_i}{x_i + y_i} \right) * (1 - x_i) + (1 - y_i - z_i) \right) * \left(q_{mi} + q_{fi} \right) \right] \quad (6)$$

$$w_{fi} = \left[(1 - epp) * \left(\left(\frac{y_i}{x_i + y_i} \right) * (1 - x_i) + (1 - y_i - z_i) \right) * \left(q_{mi} + q_{fi} \right) \right] + \left[epp * \left(\left(\frac{y_i}{x_i + y_i} \right) * (1 - x_i) + (1 - y_i - z_i) \right) * \left(q_{m1} + q_{fi} \right) \right] \quad (7)$$

To find the evolutionarily stable investments in conflict, we calculated the partial derivatives $\partial w_{m1}/\partial x_1$, $\partial w_{f1}/\partial y_1$, $\partial w_{f1}/\partial z_1$, $\partial w_{mi}/\partial y_i$, $\partial w_{mi}/\partial z_i$, $\partial w_{fi}/\partial x_i$ and solved for the conditions under which all are simultaneously equal to zero (details in Appendix 1.1).

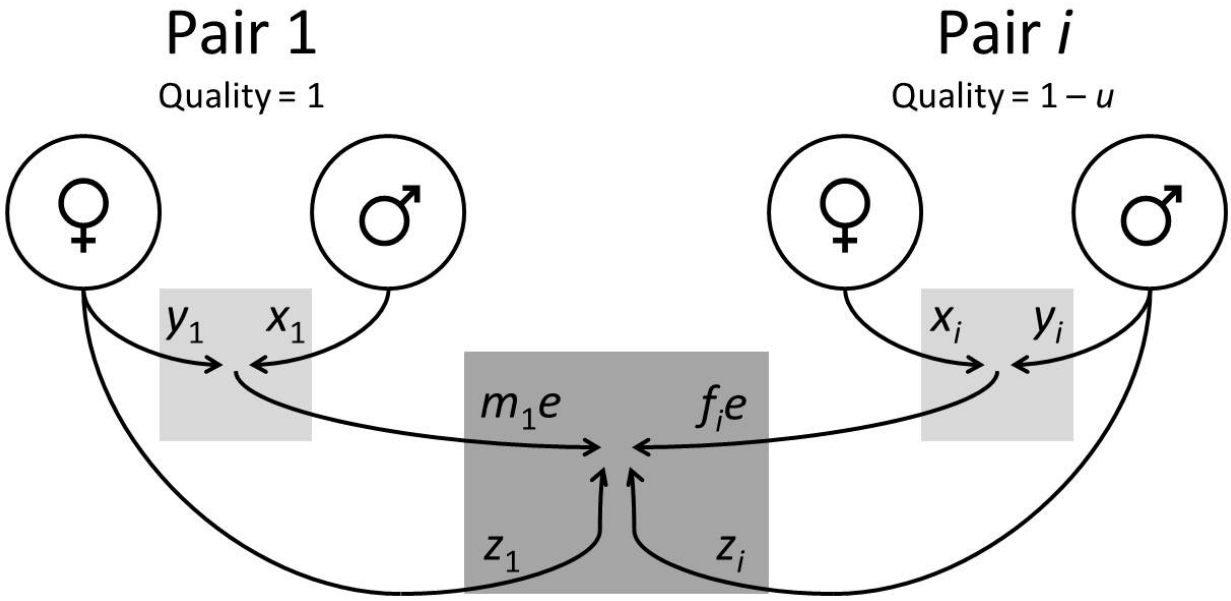

Figure 1.1 The possible investments in conflict in the 2-pair tug-of-war over paternity. y_1, Female 1's (F1) investment in *allocation conflict* (light gray) over the proportion of his energy Male 1 (M1) invests in pursuing EPCs with Female *i* (F*i*). z_1, F1's investment in *interference conflict* (dark gray) over Male 1's success in obtaining EPCs with F*i*. x_1, Male 1's investment in allocation conflict over the proportion of his energy he invests in pursuing extra-pair copulations (EPCs) with F*i*. m_1e, the proportion of M1's energy that he invests in pursuing EPCs with F*i*, which is determined by the allocation conflict between F1 and M1: $m_1e = (x_1 / (x_1 + y_1))*(1 - x_1)$. y_i, Male *i*'s (M*i*) investment in allocation conflict over the proportion of her energy Female *i* (F*i*) invests in pursuing extra-pair copulations (EPCs) with M1. z_i, M*i*'s investment in interference conflict over F*i*'s success in obtaining EPCs with M1. x_i, F*i*'s investment in allocation conflict over the proportion of her energy she invests in pursuing EPCs with M1. f_ie, the proportion of F*i*'s energy that she invests in pursuing EPCs with M1, which is determined by the allocation conflict between F*i* and M*i*: $f_ie = (x_i / (x_i + y_i))*(1 - x_i)$. *epp*, the overall proportion

of Pair 2's brood that is sired by M2, is determined by the investments in interference conflict: $epp = (m_1e + f_ie) / (m_1e + f_ie + z_1 + z_i)$. qm_1, the quality of M1. qf_1, the quality of F1. qm_2, the quality of M2. qf_2, the quality of F2. Here, we assume $qm_1 = qf_1 = 1$ and $qm_2 = qf_2 = 1 - u$.

RESULTS AND DISCUSSION

At equilibrium, the high-quality female's investment in interference conflict is equal to zero. This first major result indicates that, when lower-quality pairs are interacting with a single higher-quality pair, the high-quality female is not selected to show mate-guarding behavior. Additionally, the low-quality female(s) is not selected to invest in seeking EPCs where that investment trades off against her investment in parental care. The high-quality male does not invest in mate guarding because, by our assumption, his mate will not accept EPCs from any other male. However, the low-quality male(s) is selected to invest significantly in mate guarding (Figure 1.2), consistent with empirical results indicating that less-preferred males guard their mates more intensively (Kempenaers, Verheyen, and Dhondt 1995).

Low-quality males may benefit from breeding near each other because EPP per brood declines as the number of lower-quality pairs with which the high-quality pair interacts increases (Figure 1.3; assuming $qm_1 = qf_1 = 1$ and $qm_2 = qf_2 = 1 - u$). This pattern makes intuitive sense because the high-quality male divides his available EPC-seeking effort across a larger number of pairs, and thus does not achieve as much EPP in any one brood.

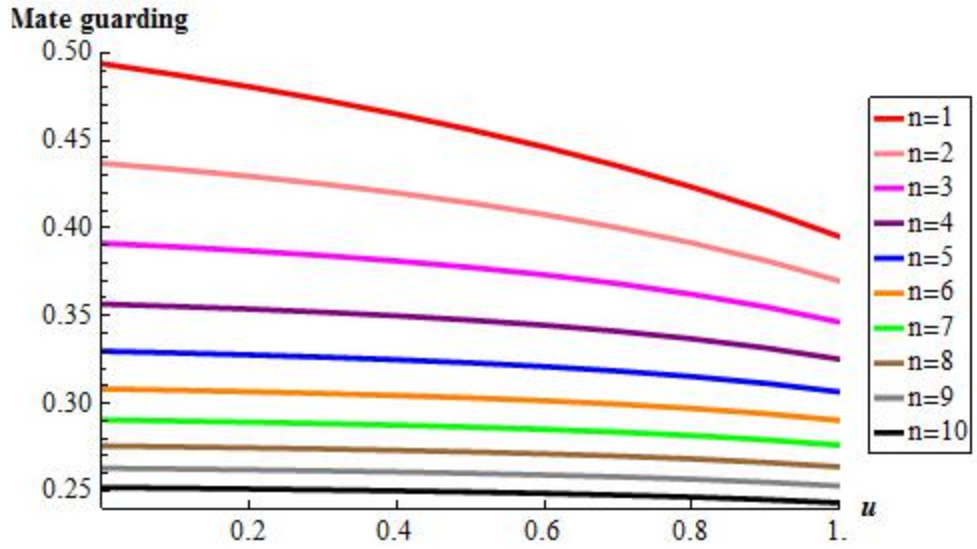

Figure 1.2 A low-quality male's investment in mate guarding (z_i) declines with the number of low-quality pairs that interact with the high-quality pair. Mate guarding also declines as the quality differential (u) between the two pairs increases, reflecting the high-quality male's decreased investment in attempting to copulate with the low-quality female, as this investment trades off against his parental investment.

The fitnesses of both the high-quality male and the low quality males increase as the number of low-quality pairs increases (Figure 1.4). The high-quality male benefits from having a greater number of broods available in which he can gain EPP, while still retaining (by our assumption) complete paternity in his own brood. The low-quality males benefit from the dilution effect of distributing the high-quality male's extra-pair mating effort across more broods, thus decreasing the paternity loss suffered by each male. This result suggests that, when a high-quality male is present, low-quality males each selfishly seeking to minimize paternity loss in his own brood may do best by clustering near the high-quality male, and further that the high-quality male also

benefits from this behavior. Through the mechanism, the hot-not effect could contribute to the formation of hidden leks, and help to stabilize coloniality.

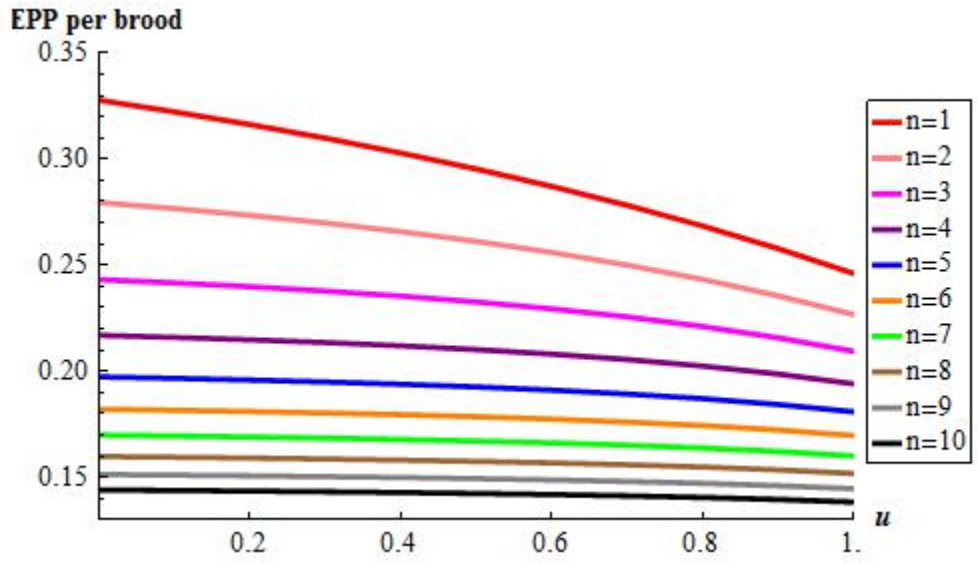

Figure 1.3 The percentage of young sired by the high-quality male in each low-quality male's nest (EPP per brood) decreases with the difference in quality of the two pairs (u) for all values of n, the number of lower-quality pairs with which the high-quality pair interacts. However, as n increases, EPP per brood becomes decreasingly sensitive to the quality differential.

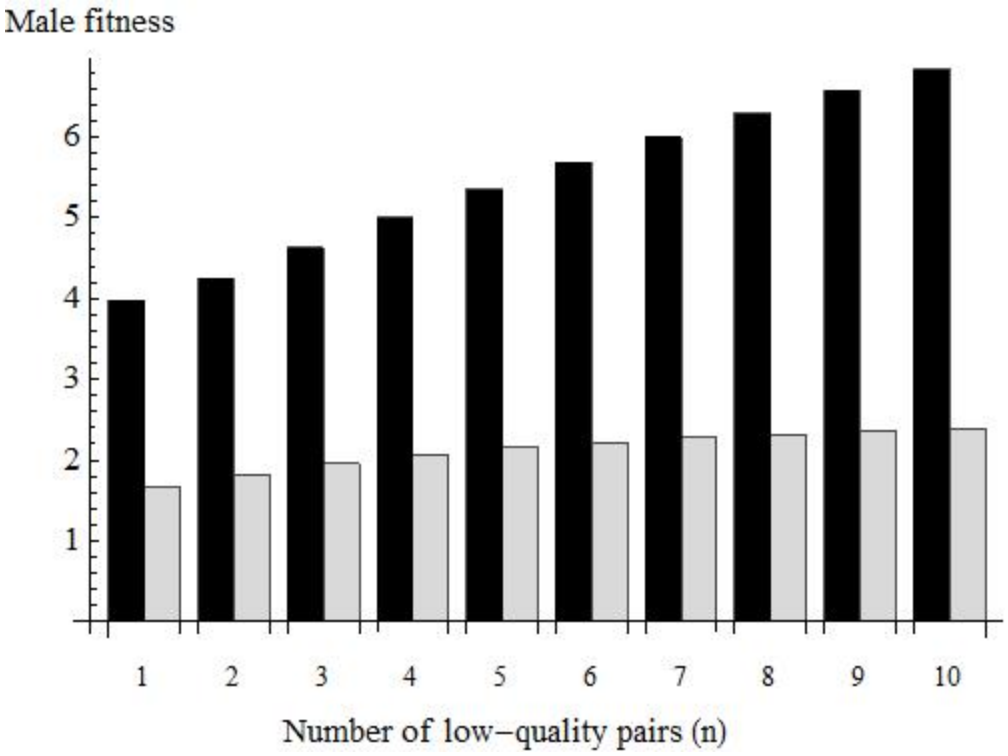

Figure 1.4 Fitness of both the high-quality male (black bars, Equation 4) and each low-quality male (grey bars, Equation 6) increases with the number of interacting pairs. Here, we set q_{m1} = q_{f1} = 1 and q_{m2} = q_{f2} = 0.8 (i.e., u = 0.2).

Predicted average EPP rates for n=1 to n=10 range from 12.3% to 18.6%, a range strikingly close to recorded average cross-species EPP rates of 11.13% in temperate (Griffith, Owens, and Thuman 2002; Macedo, Karubian, and Webster 2008) and 17.9% in tropical species (Macedo, Karubian, and Webster 2008). Interaction units of from 2 to 11 pairs are likely biologically realistic because a single male rarely gains EPP in more than 2 broods in empirical studies (Table 1.2). Average EPP rate across the set of interacting pairs is highest between n=2 and n=5 (Figure 1.5), indicating that populations in which the effective interaction unit comprises a small number of pairs will have higher average EPP. Testing this prediction empirically requires determining

how many pairs effectively interact with one another in each population; this could be achieved by observing extra-pair copulations either naturally or in the context of a male removal experiment (Dickinson 1997).

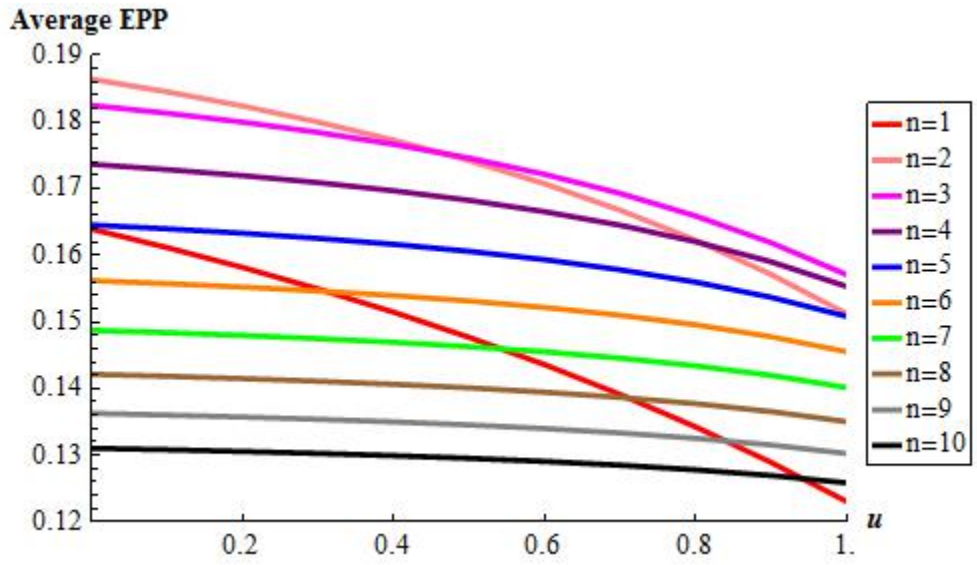

Figure 1.5 The number of lower-quality pairs with which the high-quality pair interacts (n) interacts with the difference in quality of the two pairs (u) such that, although the average extra-pair paternity rate decreases as u increases for all values of n, this decrease is sharper for smaller n values. The EPP rates displayed here are lower than those in Figure 1.3 because the average EPP is calculated including the high-quality pair's brood as well as the low-quality pair(s)'s brood(s).

When we relaxed the positive assortative mating assumption by allowing the quality of the female mated to the high-quality male to decrease relative to that of the females mated to low-quality males, we found that the high-quality male's investment in the allocation tug-of-war (x_1) increases as his mate's quality decreases relative to the other females' (see Appendix 1.1). This

means that the high-quality male invests more heavily in obtaining energy to seek EPCs when his mate is relatively low-quality. Reflecting this increased investment by the high-quality male, average EPP increases as his mate's quality decreases relative to the other females' (Figure 1.6). This instance of apparent male choosiness (Edward and Chapman 2011) is explained by the fitness tradeoffs the high-quality male faces in attempting to gain EPCs.

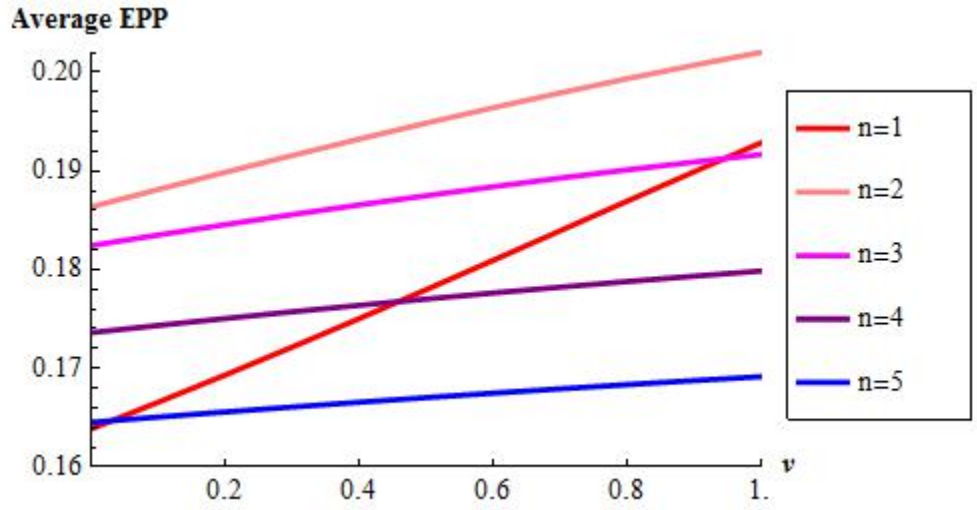

Figure 1.6 Average EPP increases as the quality of the high-quality male's mate declines relative to the quality of the extra-pair female(s).

Because as many as five EP males may sire young in the same brood (Ferretti et al. 2011), an interesting possible extension of this model would test how allowing multiple EP males to compete for paternity in a single brood affects predicted EPP rate. However, empirical data showing that the average number of extra-pair sires in a single brood is often close to 1 (Table 1.2) suggest that the current model is suitable for many species. Another possible extension would allow the high-quality male's mate to accept EPCs, capturing the situation when the same male both loses within-pair paternity and gains EPP in a single breeding bout (Table 1.1). This

relaxation of the assumption that females will accept EPCs only with males that are higher quality than their mates is justified if, e.g., females gain fertility insurance (Gibson and Jewell 1982) from mating with extra-pair males. Comparing the predictions of these extended models to the simple version we present here could motivate important cross-species tests.

The hot-not hypothesis, based on our model finding that both high- and low-quality males may benefit when low-quality males cluster their breeding territories near a high-quality male, represents an important and testable alternative explanation for "hidden leks" (Wagner 1997) in socially monogamous bird populations. Further, a population's EPP rate, which is the outcome of the conflict we model here, can have important implications for its evolutionary trajectory, given that genetically monogamous species may be more likely to evolve complex social behaviors such as cooperative breeding (Boomsma 2009; Cornwallis et al. 2010; Fromhage and Kokko 2011). Thus, the model we presented here provides a predictive framework for studying behaviors that are both widespread and evolutionarily influential.

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Table 1.2 The minimum, maximum, and average number of extra-pair sires (EPS) per brood (only broods that contain > 0 extra-pair young were used to calculate the average) in a subset of species with data available. INF, insufficient information to calculate.

Order	**Family**	**Species**	**EPS min**	**EPS max**	**Avg # of EPS per brood**	**Source**
Anseriformes	Anatidae	*Cygnus atratus*	1	3	INF	(Kraaijeveld et al. 2004)
Passeriformes	Turdidae	*Sialia curricoides*	1	4	1.4	(Balenger et al. 2009)
Passeriformes	Turdidae	*Sialia mexicana*	1	2	INF	(Ferree et al. 2010; Ferree and Dickinson 2011)
Passeriformes	Parulidae	*Dendroica caerulescens*	1	2	1.03	(Webster, Chuang-Dobbs, and Holmes 2001)
Passeriformes	Parulidae	*Geothylpis trichas*	1	2	1.333	(Guzy and Ritchison 1999; Thusius et al. 2001)
Passeriformes	Parulidae	*Setophaga ruticilla*	1	2	1.22	(Perreault, Lemon, and Kuhnlein 1997)
Passeriformes	Paridae	*Parus caeruleus*	1	3	1.33	(Delhey et al. 2003)
Passeriformes	Paridae	*Poecile atricapillus*	1	2	1.211	(Mennill 2004)
Passeriformes	Paridae	*Parus major*	1	2	1.167	(Strohbach et al. 1994)
Passeriformes	Hirundinidae	*Tachycineta bicolor*	1	5	2.1	(Dunn, Lifjeld, and Whittingham 2009)
Passeriformes	Promeropidae	*Promerops cafer*	1	2	1.342	(McFarlane et al. 2010)
Passeriformes	Sylviidae	*Locustella luscinioides*	1	2	1.33	(Neto, Hansson, and Hasselquist 2010)
Passeriformes	Hirundinidae	*Tachycineta leucorrhoa*	1	4	INF	(Ferretti et al. 2011)
Passeriformes	Hirundinidae	*Hirundo rustica*	1	3	1.35	(Kleven et al. 2006)
Passeriformes	Hirundinidae	*Delichon urbica*	1	1	1	(Whittingham and Lifjeld 1995)
Passeriformes	Muscicapidae	*Ficedula hypoleuca*	1	2	INF	(Canal, Potti, and Dávila 2011)
Passeriformes	Emberizidae	*Emberiza citrinella*	1	2	1.05	(Sundberg and Dixon 1996)
Passeriformes	Tyrannidae	*Empidonax virescens*	1	2	1.385	(Woolfenden, Stutchbury, and Morton 2005)
Passeriformes	Fringillidae	*Carpodacus erythrinus*	1	3	1.19	(Albrecht et al. 2007)
Passeriformes	Timaliidae	*Paradoxornis webbianus*	1	1	1	(Lee et al. 2009)
Passeriformes	Rhipiduridae	*Rhipidura albiscapa*	1	2	1.25	(Hoffman et al. 2010)
Passeriformes	Pachycephalidae	*Pachycephala pectoralis*	1	2	1.067	(Van Dongen and Mulder 2009)

APPENDIX 1.1

SUPPLEMENTARY METHODS

1. Solving the model

After we had calculated the partial derivatives $\partial w_{m1}/\partial x_1$, $\partial w_{f1}/\partial y_1$, $\partial w_{f1}/\partial z_1$, $\partial w_{mi}/\partial y_i$, $\partial w_{mi}/\partial z_i$, $\partial w_{fi}/\partial x_i$, we used the NSolve command in the program Mathematica 8.0 (Wolfram Research, Champaign, IL, U.S.A.) to find the values of x_1, y_1, z_1, x_i, y_i, and z_i at which all of the partial derivatives are equal to zero (having first specified values for the variables qm_1, qf_1, qm_i, qf_i, and n; we used a range of values to control for differences in results).

The NSolve command indicated that no consistent solution for the set of equations exists. We checked this result using the Reduce command, which gave the same result. We interpreted this to mean that one or more of the investment variables goes to zero at equilibrium, and eliminated variables to test this.

The first variable that we eliminated was the high-quality female's investment in interference conflict, z_1. We reformatted the fitness functions accordingly, solved for the new set of partial derivatives, and used the NSolve command to find the values of x_1, y_1, x_i, y_i, and z_i at which all of the partial derivatives are equal to zero. The NSolve command now returned results, but these did not include a set of solutions comprised only of values fitting the model's parameters (where any investment in conflict = a, the model requires $0 \leq a \leq 1$).

Next, we eliminated the variables representing the *i*th male's and *i*th female's investments in allocation conflict, x_i and y_i, respectively. We had to eliminate both variables at once rather than

one at a time because investment in conflict by one party but not the other cannot be an evolutionarily stable strategy in a tug-of-war model(Cant 2012). Again, we reformatted the fitness functions, solved for the new set of partial derivatives, and used the NSolve command to find the values of x_1, y_1, and z_i at which all of the partial derivatives are equal to zero. We now found that, for all starting values of the variables qm_1, qf_1, qm_i, qf_i, and n that we tried, there was one set of values in each solution set that fit the model requirements. Accordingly, we used this version of the model for our subsequent analyses.

2. The effect of the quality differential between pairs and the number of pairs on investments in conflict

To examine these effects, we substituted qm_1=1, qf_1=1, qm_i=1 – u, and qf_i = 1 – u into the model and calculated the partial derivatives as above. Then, we used the Solve command to find the value of y_1 at which $\partial w_{f1}/\partial y_1 = 0$,

$$-\mathrm{x}_1 + \sqrt{-(-1+\mathrm{x}_1)\mathrm{x}_1} \tag{1}$$

and the formula for z_i at which $\partial w_{mi}/\partial z_i = 0$,

$$\frac{(-1+\mathrm{x}_1)\mathrm{x}_1 + \sqrt{(-1+\mathrm{x}_1)\mathrm{x}_1(\mathrm{x}_1(-1-2n+\mathrm{x}_1) - 2n\mathrm{y}_1)}}{n(\mathrm{x}_1+\mathrm{y}_1)} \tag{2}$$

We substituted (1) into (2) to obtain the following expression for z_i:

$$\frac{(-1+\mathrm{x}_1)\mathrm{x}_1 + \sqrt{(-1+\mathrm{x}_1)\mathrm{x}_1((-1+\mathrm{x}_1)\mathrm{x}_1 - 2n\sqrt{-(-1+\mathrm{x}_1)\mathrm{x}_1})}}{n\sqrt{-(-1+\mathrm{x}_1)\mathrm{x}_1}} \tag{3}$$

We then defined g as $\partial w_{m1}/\partial x_1$ evaluated when y_1 is equal to (1) and z_i is equal to (3).

Using the FindRoot command, we solved for the value of x_1 where g is equal to zero while 1) holding n constant while u was allowed to vary, and 2) holding u constant while n was allowed to vary. We found that the high-quality male's investment in conflict 1) decreased as u increased, and 2) increased as n increased.

3. Relaxing the positive assortative mating assumption

In order to test the effect of the relative qualities of the high-quality male's mate and the low-quality female(s) on extra-pair paternity rates, we followed the same procedure as outlined in Section 2, above, using different sets of values for qm_1, qf_1, qm_i, and qf_i.

a) Positive assortative mating: qm_1=1, qf_1=1, qm_i=1 – u, and qf_i = 1 – u. The high-quality male's investment in conflict (x_1) decreased as u increased, suggesting that a lower relative quality of the extra-pair female selects for decreased investment in obtaining energy to invest in extra-pair matings

b) The females are equal in quality: qm_1=1, qf_1=1, qm_i=1 – u, and qf_i = 1. The high-quality male's investment in conflict (x_1) did not change with u, suggesting that the relative quality of the rival male does not affect the high-quality male's investment.

c) Disassortative mating: qm_1=1, qf_1=1 – u, qm_i=1 – u, and qf_i = 1. The high-quality male's investment in conflict (x_1) increased as u increased, suggesting that a lower relative quality of his own mate selects for increased investment in obtaining energy to invest in extra-pair matings.

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CHAPTER 2

KIN STRUCTURE INCREASES THE BENEFITS OF INDEPENDENT BREEDING RELATIVE TO HELPING FOR MALE POTENTIAL HELPERS IN POPULATIONS WITH NON-ZERO EXTRA-PAIR PATERNITY RATES

Caitlin A. Stern

SUMMARY

Among bird species in which more than two individuals cooperatively rear young, both male helpers at the nest and paternity loss by male breeders are widespread (Cockburn 1998). Two hypotheses attempt to explain the influence of paternity loss on the costs and benefits of helping behavior. The monogamy hypothesis arose within the context of female helping in insects (Page and Metcalf 1982; Boomsma 2007; Boomsma 2009) and incorporates reduction in relatedness due to maternal promiscuity into measures of the inclusive fitness benefits of helping behavior. The inclusive fitness comparison hypothesis arises from research on male helper systems (Dickinson, Koenig, and Pitelka 1996) and takes a comparative approach incorporating the effect of both the mother's promiscuity and the promiscuity of a male's own mate, assuming that males are able to assess whether helping or breeding independently is the best option in terms of maximizing inclusive fitness. Inclusive fitness comparisons in western bluebirds, *Sialia mexicana*, explained males', but not females' help as breeding-age adults (Dickinson, Koenig, and Pitelka 1996). The mathematical model and inter-species comparisons presented here generalize findings based on inclusive fitness comparisons and corroborate evidence based on a single-species test using inter-species comparisons. However, neither the inclusive fitness

comparison hypothesis nor the monogamy hypothesis accounts for the possible influence of kin structure on the relative benefits of helping versus breeding. This factor is important because populations of many species both with and without documented cooperative breeding exhibit kin structure (Hatchwell 2010). The model predicts that kin structure decreases the costs of independent breeding for young males such that breeding may yield higher inclusive fitness benefits than helping even in the face of paternity loss. The primary reason for this is intuitive: if males have same-sex relatives (e.g., brothers) nearby that become extra-pair sires at their nests, this lessens the reduction of relatedness due to paternity loss. Together, these results suggest that 1) an hypothesis for the evolution of cooperative breeding in birds that takes into account the promiscuity of potential mates can explain the bias towards male helpers when helpers do not gain direct within-group reproduction, and 2) kin structure may decrease the costs of independent breeding relative to helping in some contexts, a finding that may help explain the presence of kin structure in populations without documented cooperative breeding behavior.

INTRODUCTION

The monogamy hypothesis for the evolution of cooperative breeding (Page and Metcalf 1982; Boomsma 2007; Boomsma 2009) postulates a causal role for female promiscuity in the transition between independent and cooperative breeding. In the scenario of interest, an individual has two options: 1) remain in his or her natal group and help to raise siblings, forgoing direct reproduction; or 2) disperse and attempt to breed independently. The monogamy hypothesis states that the number of males from whom the individual's mother receives fertilizations affects this decision due to the impact of genetic polyandry on sibling relatedness: in diplo-diploid systems, if the mother is monogamous, the individual will have a coefficient of relatedness with

its siblings equal to 0.5, while if the mother is polyandrous, the individual's coefficient of relatedness with its siblings will be lower than 0.5 and may approach 0.25 (half-siblings, under complete genetic polyandry; Hamilton 1964a; Hamilton 1964b). An individual is related to its own offspring by 0.5, so independent breeding will be more strongly selected for when the mother is likely to mate with multiple males. This idea was originally articulated in the context of social evolution in hymenopteran insects (Page and Metcalf 1982), and only later termed the "monogamy" hypothesis (Boomsma 2007; Boomsma 2009).

A recent cross-species test of this idea expanded its taxonomic scope by examining the role of promiscuity in the evolution of helping behavior in facultative cooperatively breeding birds (Cornwallis et al. 2010). However, an obstacle to testing the monogamy hypothesis in species with male helping is that the monogamy hypothesis does not account for the effect of female promiscuity on the focal individual's outside option (independent breeding) when the focal individual is male. Male helpers occur in all 36 of the avian species classified as having a cooperative breeding system and used to test the monogamy hypothesis by Cornwallis et al. (2010) (Appendix 2.1), making consideration of this issue essential.

If genetic polyandry occurs in a population, a dispersing male who is successful in acquiring a mate and breeding independently may end up raising offspring that are not his own as a result of his mate's promiscuity (Dickinson, Koenig, and Pitelka 1996). Therefore, this independently breeding individual will not be related to all of his putative offspring by 0.5, and this decreased effective reproductive output must be considered when comparing the costs and benefits of each option (Dickinson, Koenig, and Pitelka 1996). Because the indirect benefits of helping will also

be reduced if extra-pair offspring occur in the father's nest, paternity loss must be incorporated into calculations of the relative inclusive fitness benefits of helping versus breeding independently when determining whether it is beneficial for sons to help. I term this alternative, first proposed by Dickinson et al. (1996), the "inclusive fitness comparison" hypothesis, because it suggests that males compare the inclusive fitness advantages based upon the influence of extra-pair paternity on the relative inclusive fitness benefits of helping versus breeding independently. This hypothesis is an important extension of the original idea that multiple mating by mothers may decrease sibling relatedness and thus decrease the inclusive fitness benefits of helping, considering both the mother's promiscuity and the prospective female mate's promiscuity and weighing the relative fitness consequences of breeding independently versus helping.

Here I present a more complete model that extends the inclusive fitness comparison hypothesis beyond comparison of an individual's independent versus a helped nest to also include the relative costs and benefits of losing paternity to a relative versus a nonrelative. Allowing for the possibility of paternity loss by a potential helper male leads to an important and overlooked consideration: if a male that opts to breed independently settles near male kin, he may lose paternity to kin as well as non-kin. The degree of kin structure, or the extent to which related individuals are clustered spatially, may thus affect the inclusive fitness benefits of independent breeding relative to helping. Because populations of many avian species both with and without documented cooperative breeding exhibit kin structure (Hatchwell 2010), considering the effects of kin structure on the costs and benefits of independent breeding relative to helping both increases the realism of the model presented here and gives us the opportunity to examine the

interactions between kin structure and genetic mating system in influencing the expression of cooperative behavior.

I develop a simple, general mathematical model to illustrate these points and show that the predictions of the model accord with 1) the predictions of the monogamy hypothesis with respect to potential female helpers and 2) the inclusive fitness comparison hypothesis with respect to potential male helpers. I then present a cross-species empirical test of the inclusive fitness comparison hypothesis, suggesting that the occurrence of extra-pair paternity may be an important factor influencing the sex ratio of helpers. Finally, I use the model to examine the effects of kin structure on the relative benefits of helping behavior for males, showing that kin structure increases the benefits of independent breeding relative to helping such that males with the option of breeding in a kin-structured population will require a higher level of maternal monogamy to stay and help than will males without this option.

RESULTS AND DISCUSSION

1. Fitness functions: staying and helping versus dispersing and breeding

The inclusive fitness an individual gains when he or she stays on the natal territory (assuming helpers gain no direct reproduction in their parents' broods), S, is given by the number of additional siblings produced as a result of the helper's help (N_s) multiplied by the sum of 1) the proportion of young in the parents' brood that are the helper's full siblings (p; this term takes into account the possibility that the helper is an extra-pair offspring, Appendix 2.2), multiplied by the individual's relatedness to his or her full siblings (r_{full}); and 2) the proportion of young in

the parents' brood that are the helper's half-siblings ($1 - p$), multiplied by the individual's relatedness to his or her half-siblings (r_h):

$$S = N_s\left[\left(pr_{full}\right) + \left((1-p)r_h\right)\right] \quad (1)$$

In outbred, diplo-diploid systems r_{full} and r_h are equal to 0.5 and 0.25, respectively. I assume incest avoidance (males do not mate with mothers and females do not mate with social fathers), the absence of joint-nesting by mothers and daughters (as sometimes occurs in e.g. Seychelles warblers, *Acrocephalus sechellensis*; Richardson, Burke, and Komdeur 2002), and the absence of intraspecific brood parasitism. I also assume that male and female helpers produce equal numbers of younger siblings when helping at the nest.

When the individual deciding whether to stay or disperse is a female, the inclusive fitness she gains through independent breeding (F) consists of the number of offspring she produces (N_f) multiplied by her relatedness to her own offspring (r_f):

$$F = N_f r_f \quad (2)$$

However, when the individual deciding whether to stay or disperse is a male, the inclusive fitness he gains through independent breeding (M) consists of the number of offspring he produces (N_m) multiplied by the sum of 1) his relatedness to his own offspring (r_m) multiplied by the proportion of young in his brood that he sires (q), and 2) his relatedness to offspring sired by other males (r_e) multiplied by the proportion of his brood that is sired by other males ($1 - q$):

$$M = N_m\left[(qr_m) + \left((1-q)r_e\right)\right] \quad (3)$$

In diplo-diploid systems with low kin structure, r_m and r_e are equal to 0.5 and 0, respectively. Also note that I disregard in this formulation any additional fitness the focal male himself may gain through extra-pair paternity; this is because I assume that the focal male would gain the

same amount of fitness through fertilizations of other males' mates as a helper and as a breeding male, thus resulting in cancellation of this fitness component when comparing fitness between helpers and breeders. However, if data suggest that breeding status confers an automatic advantage in gaining such fertilizations, this assumption can easily be relaxed by adding the term $(N_e r_m)$ to Equation 3, where N_e is the number of extra-pair young sired by the focal male.

2. When are females selected to stay and help?

Females are selected to stay and help rear siblings when $S > F$. To find the threshold level of p (the proportion of young in the parents' brood that are fullsiblings), p^*, above which the female should stay, I set Equation 1 > Equation 2 and solved for p, obtaining the p^* value

$$p^* > \frac{\left(N_f r_f - N_s r_h\right)}{\left(N_s r_{full} - N_s r_h\right)} \tag{4}$$

With r_{full}=0.5, r_h=0.25, and r_f=0.5 (diplo-diploid, out-bred system), this simplifies to

$$p^* > 2\left(\frac{N_f}{N_s}\right) - 1 \tag{5}$$

Thus, the value p^* below which the focal female is selected to disperse and breed independently depends on the ratio of the number of offspring she is expected to produce as an independent breeder (N_f) to the number of siblings she is expected to produce as a helper (N_s).

When the female produces fewer than half as many offspring as an independent breeder than siblings as a helper, or $\frac{N_f}{N_s} < 0.5$, the female is selected to stay and help for any $p > 0$. However, as the value of the ratio $\frac{N_f}{N_s}$ increases past 0.5, staying and helping is only favored for increasingly large values of p. When the female produces a number of offspring as an independent breeder

equal to the number of additional siblings she produces as a helper, or $\frac{N_f}{N_s} = 1$, the female is never selected to stay and help, given that $p > 1$, the proportion of young in her parents' brood that are her full siblings, cannot be greater than 1.

Thus, as the value of the female's outside option (the number of offspring she can expect to produce as an independent breeder) increases relative to her within-group option, the degree of maternal monogamy required to select the focal female to stay and help also increases. For a given ratio of the values of the outside option to the within-group option, higher maternal monogamy will result in an increased probability that the focal female is selected to stay and help, in accordance with the predictions of the monogamy hypothesis.

3. When are males selected to stay and help?

Males are selected to stay and help rear siblings when $S > M$. To find the threshold level of p, p^*, at which the fitness consequences of the male's options are equal, I set Equation 1 > Equation 3 and solved for p, obtaining the p^* value

$$p^* > \frac{(N_m r_e - N_m q r_e + N_m q r_m - N_s r_h)}{(N_s r_{full} - N_s r_h)} \quad (6)$$

With r_{full}=0.5, r_h=0.25, r_m=0.5, and r_e=0, this simplifies to

$$p^* > 2q\left(\frac{N_m}{N_s}\right) - 1 \quad (7)$$

Here, as when the focal individual is female, the value of p^* (the proportion of offspring in the parents' brood that are full siblings) below which the focal male is selected to disperse and breed independently depends on the ratio of the number of offspring he is expected to produce as an independent breeder (N_m) to the number of offspring he is expected to produce as a helper (N_s).

However, when the focal individual is male, p^* also depends on q, the expected proportion of the male's own brood that he sires. The value of p^* increases with both the ratio $\frac{N_m}{N_s}$ and q: as the value of the male's outside option (the number of offspring he can expect to produce as an independent breeder) increases relative to the value of his within-group option, and as the proportion of the male's own young he can expect to sire as an independent breeder increases, the degree of maternal monogamy required to select the focal male to stay and help also increases. The predicted effect of q accords with the predictions of the inclusive fitness comparison hypothesis.

4. Selection for female helping requires higher maternal monogamy than selection for male helping when male breeders do not gain complete paternity

The staying condition (p^*) is less stringent, i.e. a lower level of maternal monogamy is required to select for staying and helping, for males than for females when Equation 5 is greater than Equation 7, assuming that males and females have equal numbers of expected offspring as breeders ($N_m = N_f$). By setting Equation 5 > Equation 7 and solving for q, I find that, whenever males do not have complete paternity in their independent broods ($q < 1$), their staying condition is less stringent than that for females. When males do have complete paternity in their own broods ($q = 1$), the staying conditions for males and females are equal. However, note that the staying condition is never *more* stringent for males than for females, as q cannot exceed 1. Thus, the model predicts that males will be equally or more likely than females to become helpers, but not less likely, when males and females have equal expected offspring numbers as breeders.

The assumption that males and females produce equal numbers of expected offspring as breeders may not hold in all populations. For example, if dispersing males are significantly less likely to obtain mates than are dispersing females (due to e.g. a male-biased sex-ratio; Pruett-Jones and Lewis 1990), then the expected number of offspring produced by dispersing males will be smaller than that produced by dispersing females (i.e., $N_m < N_f$). A decrease in N_m with respect to N_f results in a less stringent staying condition for males as compared to females, and thus an increased likelihood of males versus females becoming helpers, even if $q = 1$.

5. Helping by young males is more likely to occur when younger males lose more paternity than older males

In many bird species, empirical evidence suggests that younger males suffer higher paternity losses than do older males (Perreault, Lemon, and Kuhnlein 1997; Richardson and Burke 1999). Indeed, age may be the factor most consistently associated with extra-pair paternity across species (Green, Peters, and Cockburn 2002), with older males losing less within-pair paternity (Perreault, Lemon, and Kuhnlein 1997; Richardson and Burke 1999) and gaining more extra-pair paternity (Weatherhead and Boag 1995; Sundberg and Dixon 1996; Perreault, Lemon, and Kuhnlein 1997; Richardson and Burke 1999; Johnsen et al. 2001; Bitton, O'Brien, and Dawson 2007; Bouwman et al. 2007; Lehtonen, Primmer, and Laaksonen 2009; Ferree and Dickinson 2011). This pattern could arise through female preference for older extra-pair mates (Ferree and Dickinson 2011), or an age-related disparity in the ability to exploit extra-pair mating opportunities (Weatherhead and Boag 1995).

In order to examine the effects of the relationship between the male's expected paternity as a breeder (q) and the proportion of young in his parents' brood that are his full siblings (p) on the costs and benefits of helping behavior, we can re-write the simplified staying condition for males given in Equation 7 as follows:

$$\left(\frac{N_m}{N_s}\right) < \left(\frac{p^* + 1}{2q}\right) \quad (8)$$

Here, the inclusive fitness benefits of helping outweigh the costs when the ratio of the number of young raised as a breeder to the number of young raised as a helper (hereafter, "*N*-ratio") is smaller than a number determined by the values of p and q (hereafter, "*N*-ratio threshold"). When the *N*-ratio threshold is greater than one, the inequality in Equation 8 holds true even when the male can expect to produce as many young as a breeder than siblings as a helper (*N*-ratio = 1). Thus, larger values of the *N*-ratio threshold indicate that helping is more likely to occur, because a greater range of possible *N*-ratio values are consistent with the inequality.

We can show algebraically that, for a given value of p, the *N*-ratio threshold is always larger when $p > q$ than when $p < q$ (Appendix 2.3). This result indicates that the cost-benefit balance is more likely to favor helping over breeding when the proportion of a focal male's parents' young that are full siblings is higher than the proportion of his own brood that are within-pair young ($p > q$) than vice versa ($p < q$). A key prediction of the model is thus that, for species meeting the assumptions of the model, helping by young males will be more likely to occur in species in which female extra-pair mating preferences favor older males than in species in which female extra-pair mating preferences favor younger males.

6. Comparative test: male helper proportion is significantly higher among species with non-zero than among species with zero extra-pair paternity

I tested the prediction that selection favors helping by males over helping by females when $q < 1$ by comparing the proportion of helpers that are male in species in which breeder males do not lose paternity to extra-group males with the proportion of helpers that are male in species in which breeder males do lose paternity to extra-group males. From among the 36 cooperative species identified by Cornwallis et al. (2010), I identified 14 species for inclusion in the analysis. Using a rule similar to that for classifying species as polygynous (Verner and Willson 1969), I considered species in which helpers gain direct within-group reproduction in >5% of cases as species in which direct fitness benefits may be an important consequence of helping behavior, and thus not suitable for inclusion in the analysis due to the exclusion of this possibility in the model. Additionally, the analysis was necessarily restricted to species for which information was available on the proportion of helpers that are male as well as the extra-group paternity rate (the proportion of young sired by males external to the social group) (Appendix 2.1).

Species in which the extra-group paternity rate was greater than 0% had a significantly higher proportion of male helpers than did species in which the extra-group paternity rate was equal to 0% (N=6, mean=0.897±0.066 for species with extra-group paternity rate >0; N=8, mean=0.649±0.052 for species with extra-group paternity rate=0; Wilcoxon rank sum test, $p = 0.017$; Figure 2.1). This result both supports the model and indicates that, among species in which helpers do not gain direct reproduction, extra-group paternity rate may be an important factor influencing the sex ratio of helpers. Because the causes of helper sex ratios are poorly

understood (Cockburn 1998), this finding may have broad importance for the study of avian cooperative breeding.

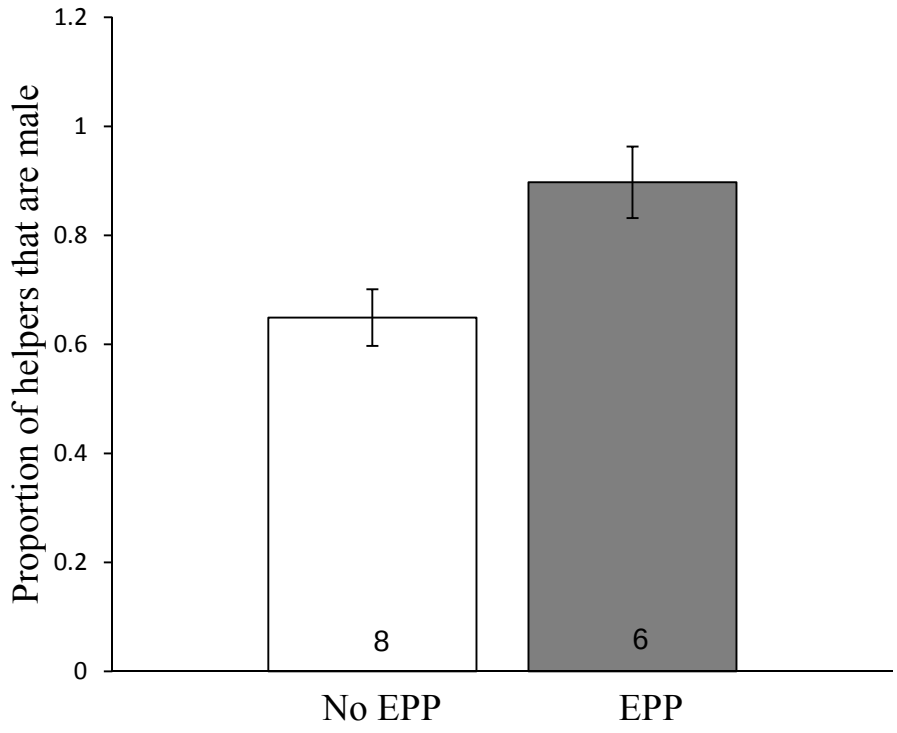

Figure 2.1 Selection favors helping by males when male breeders do not achieve complete paternity. Species in which the extra-group paternity rate was greater than 0% had a significantly higher proportion of male helpers than did species in which the extra-group paternity rate was equal to 0% (N=8, mean=0.649±0.052 for species with extra-group paternity rate=0; N=6, mean=0.897±0.066 for species with extra-group paternity rate >0; Wilcoxon rank sum test, p = 0.017). The analysis includes the 14 species among the 36 cooperative species identified by Cornwallis et al. (2010) in which <5% of young resulted from direct reproduction by helpers and for which information was available on both the proportion of helpers that are male and extra-

group paternity rate (Appendix 2.1). Numbers within bars indicate sample sizes (number of species) for each category.

7. Kin structure increases the benefits of independent breeding relative to helping

In kin-structured populations, independently breeding males may lose paternity to kin as well as to non-kin, leading to non-zero relatedness of the focal male to extra-pair young in his brood ($r_e > 0$). Thus, we can examine the effects of kin structure on a male's decision to help versus breed by relaxing the previous assumption that a male is unrelated to all extra-pair young in his brood ($r_e = 0$). Recall that the male's staying condition, or the proportion of his parents' brood that must be his full siblings in order for him to receive greater inclusive fitness benefits from helping than from breeding, is

$$p^* > \frac{N_m r_e - N_m q r_e + N_m q r_m - N_s r_h}{N_s r_f - N_s r_h} \quad (9)$$

When $r_e = 0$, this condition simplifies to

$$p^* > \frac{N_m q r_m - N_s r_h}{N_s r_f - N_s r_h} \quad (10)$$

Thus, the staying condition is more stringent in the presence than in the absence of kin structure when $N_m r_e - N_m q r_e > 0$. The latter inequality shows that kin structure will only affect the benefits of helping relative to breeding when the focal male's expected number of offspring as an independent breeder is non-zero ($N_m > 0$) and when the focal male can expect to lose a non-zero proportion of paternity to extra-pair males ($q < 1$), both conditions making intuitive sense. We can also determine that, where both of these conditions and the previous definitions of the parameters are met ($0 \leq q < 1$; $0 < r_e \leq 0.25$; $N_s > 0$), the inequality always holds true. This means that kin structure increases the benefits of breeding independently relative to helping such that

males with the option of breeding in a kin-structured population will require a higher level of maternal monogamy to stay and help than will males without this option (Figure 2.2).

In a kin-structured population, the male's mother, as well as his mate, may be fertilized by extra-pair males related to the focal male. Assuming incest avoidance, the male's mother will not accept fertilizations from his brothers or maternal uncles, but may accept fertilizations from his paternal uncles or paternal grandfather. Extra-pair mating by the male's mother with relatives of the focal male will increase the focal male's relatedness to extra-pair siblings in his parents' brood (r_h) above the level of half-siblings. However, this does not alter the mitigating effect of kin structure on the costs of paternity loss to breeding males: increased kin structure still results in increased benefits of breeding independently relative to helping.

Summary of major results

1. Across cooperatively breeding species, the proportion of male helpers is significantly higher among species with non-zero extra-pair paternity rates than among species with zero extra-pair paternity, in accordance with a prediction of the model.
2. Kin structure decreases the costs of independent breeding for young males such that breeding may yield higher inclusive fitness benefits than helping even in the face of paternity loss

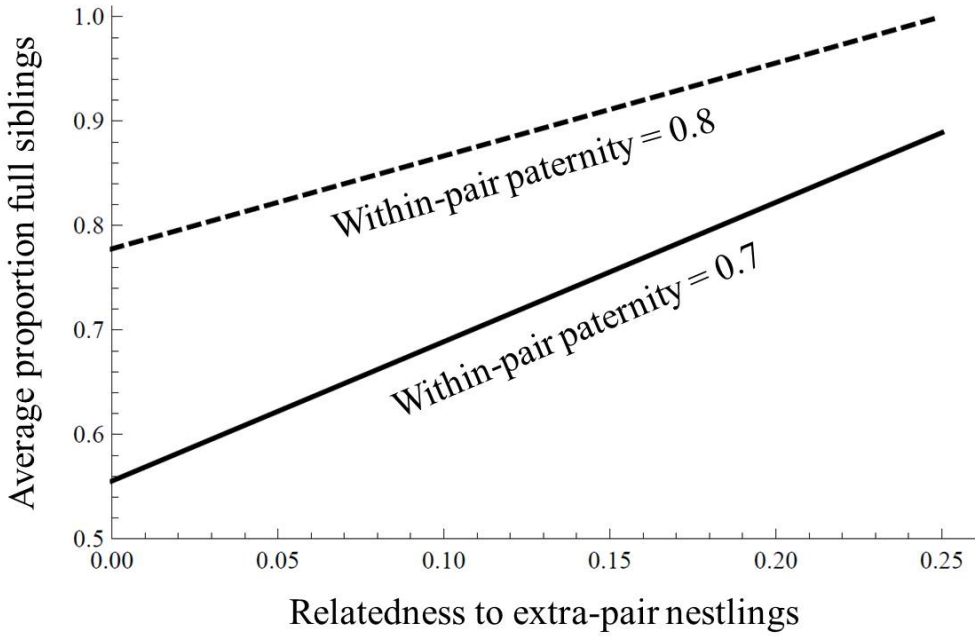

Figure 2.2 The effect of kin structure on the benefits of helping behavior for males. As a male's relatedness to the extra-pair nestlings he would raise as a breeder (r_e) increases, the average proportion of young in his parents' brood that are his full siblings must be increasingly high in order for him to gain higher inclusive fitness from helping than from breeding independently. Thus, kin structure leading to non-zero relatedness among a social male and the extra-pair young in his brood increases the benefits of breeding independently relative to helping for males.

Conclusions and implications

The contributions of this investigation are threefold. First, I highlight the important biological insights that the inclusive fitness comparison hypothesis (Dickinson, Koenig, and Pitelka 1996) adds to recent thinking on the evolution of cooperative breeding by presenting this hypothesis in a generalized mathematical form to emphasize its applicability across cooperatively breeding taxa. Second, I demonstrate the explanatory power of this generalized approach by using a cross-species comparison to test a key prediction. Third, I provide a critical extension of this

hypothesis by analyzing the potential effects of kin structure on the costs and benefits of helping behavior.

Highlighting the insights of the inclusive fitness comparison hypothesis is important because, in populations with non-zero extra-pair paternity rates, as is the case for many cooperatively breeding bird species (Cockburn 1998), both the potential paternity loss of a male and his father's paternity loss in the helped nest alter the relative inclusive fitness consequences of helping versus breeding. This element is missing from many recent theoretical investigations of the evolution of cooperative breeding. For example, one model showed that maternal monandry contributes positively to the evolution of helping behavior, but assumed that all male offspring disperse, and thus considered only female offspring to be potential helpers (Fromhage and Kokko 2011). The model presented here accords with previous inclusive fitness reasoning applied to hymenopteran taxa in predicting that, all else being equal, maternal monogamy increases selection for helping by female offspring (Page and Metcalf 1982). However, the model diverges from the monogamy hypothesis as recently articulated (Boomsma 2007; Boomsma 2009), and accords with the inclusive fitness comparison hypothesis, in predicting that the proportion of offspring a young male can expect to sire as an independent breeder affects the costs and benefits of helping behavior. Accounting for variation in the biology of different taxa – here, the prevalence of both male helpers and extra-pair paternity in cooperatively breeding birds (Cockburn 1998) – is an important step in developing general theories for the evolution of cooperative breeding and other sociobiological phenomena.

If the potential for paternity loss as an independent breeder decreases the inclusive fitness benefits of breeding versus helping for males, we expect that the proportion of helpers that are male will be higher in species with non-zero extra-group paternity loss than in species with zero extra-group paternity loss. The cross-species analysis presented above found the predicted pattern in cooperatively breeding birds. Although a previous within-species test in western bluebirds (*Sialia mexicana*) did not find support for the inclusive fitness comparison hypothesis (Dickinson and Akre 1998), the support from this comparative analysis suggests that the influence of potential paternity loss on the relative benefits of helping for males versus females bears further investigation. One reason for the difference in findings may be that within-species comparisons require individuals to make fitness-based decisions, whereas cross-species comparisons merely require an evolved level of helping in accordance with the average extra-pair paternity rate. In other words, males need not have specific information on their mate's and their mother's behavior to respond in ways that increase fitness based on the population mean.

An interesting additional result of the cross-species analysis is that, in many of the cooperatively breeding species examined, helpers of either one or both sexes obtained direct reproduction in the broods they helped such that the species did not meet the assumptions of the model, which allows for only indirect fitness gains by helpers. Among species in which helpers frequently gain within-group reproduction, one might expect that the sex more likely to gain direct reproduction would be over-represented among helpers, and empirical evidence supports this prediction (Richardson, Burke, and Komdeur 2002). Together, the latter hypothesis and the son disadvantage hypothesis may help explain the variation in helper sex ratio among cooperatively breeding bird species.

A classic and well-supported prediction in the cooperative breeding literature is that kin structure sets the stage for cooperative behavior by increasing the availability of related potential helpers (Emlen 1995). A major finding of the present study is that kin structure may select against cooperative breeding in some contexts: the model predicts that kin structure decreases the costs of independent breeding for young males such that breeding may yield higher inclusive fitness benefits than helping even in the face of paternity loss. This finding does not contradict previous predictions, as cooperative behavior other than help at the nest may be facilitated by the presence of nearby kin (MacColl et al. 2000), but instead adds to our knowledge of the potentially complex effects of kin structure on cooperative behavior. Positive feedback may occur such that as kin structure increases, the benefits of independent breeding increase, leading to a further increase in kin structure as young males are selected to establish independent territories near male relatives. Importantly, this finding may help explain the presence of kin structure in populations without documented cooperative breeding behavior (Hatchwell 2010). Even when potential helpers exist, the inclusive fitness benefits of producing descendent young while also investing in the non-descendent kin that are the result of within-brood paternity loss may select against the expression of cooperative behavior.

The model presented here combines the generality of the monogamy hypothesis and the important biological insights of the inclusive fitness comparison hypothesis, while providing an important extension in incorporating the potential effects of kin structure on the costs and benefits of cooperative behavior. Although many expansions of the model are possible, one interesting future line of investigation is how the potentially causal relationships between maternal monogamy and helper presence may influence selection on helping behavior. For

example, mother guarding (Welbergen and Quader 2006), in which a helper protects its father's paternity by defending against potential extra-pair males, could result in increased maternal monogamy. Alternatively, females may increase their promiscuity in the presence of helpers due to a decreased need to trade paternity for parental assistance (Mulder et al. 1994). These relationships require further investigation as they could importantly influence selection pressures on both genetic mating systems and cooperative breeding behavior.

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APPENDIX 2.1

List of all species identified by Cornwallis et al. (2010) as cooperative breeders, with additional information gathered on the sex of helpers, the proportion of helpers that are male, whether helpers may gain direct within-group reproduction, and the rate of extra-pair paternity. Species included in this analysis are marked with an asterisk (*).

Common name	**Scientific name**	**Sex of helpers**	**Proportion of helpers that are male**	**"Helpers" may gain direct within-group fitness**	**Extra-group paternity rate**
Seychelles Warbler	*Acrocephalus sechellensis*	Male and female (Richardson et al. 2001)	0.317 (Richardson, Burke, and Komdeur 2002)	Yes, both males and females (Richardson et al. 2001)	0.3818 (all extra-group; only one offspring sired by a male helper) (Richardson et al. 2001)
Long-tailed Tit*	*Aegithalos caudatus*	Male and female (Russell and Hatchwell 2001; Hatchwell et al. 2004)	0.856 (Russell and Hatchwell 2001)	No (Hatchwell 2002)	0.0240 (Hatchwell 2002)
Florida Scrub Jay*	*Aphelocoma coerulescens*	Male and female (Quinn et al. 1999)	0.5185 (Quinn et al. 1999)	No (Quinn et al. 1999)	0 (Quinn et al. 1999)
Mexican Jay	*Aphelocoma ultramarina*	Male and female (Brown 1970; Li and Brown 2000)	Unknown	Yes, for males (Li and Brown 2000)	0.3957 (majority within-group sires) (Li and Brown 2000)
White-throated Magpie-Jay	*Calocitta formosa*	Male and female (Berg 2005)	0.07 to 0.12 (Langen 1996; Berg 2005)	Yes, for females (unknown for males (Berg 2005)	0.3810 (floater and extra-group males) (Berg 2005)
Bicolored Wren	*Campylorhynchus griseus*	Male and female (Austad and Rabenold 1985)	0.491 (Haydock, Parker, and Rabenold 1996)	Yes, for males (Haydock, Parker, and Rabenold 1996)	0.450 (half by helpers, half by extra-group males) (Haydock, Parker, and Rabenold 1996)

Common name	Scientific name	Sex of helpers	Proportion of helpers that are male	"Helpers" may gain direct within-group fitness	Extra-group paternity rate
Stripe-backed Wren	*Campylorhynchus nuchalis*	Male and female (P.P. Rabenold et al. 1990)	0.495 (Rabenold 1985)	Yes, for males (P.P. Rabenold et al. 1990; Piper and Slater 1993)	0.1014 (6/69 by aux male and 1/69 by extra-group male) (P.P. Rabenold et al. 1990)
White-winged Chough	*Corcorax melanorhamphos*	Male and female (Heinsohn et al. 2000)	0.6471 (Heinsohn et al. 2000)	Yes, for males and rarely females (Heinsohn et al. 2000)	0 in long-term groups (Heinsohn et al. 2000)
American Crow	*Corvus brachyrhynchos*	Male and female (Townsend et al. 2009)	0.6486 (Townsend et al. 2009)	Yes, for males (Townsend et al. 2009)	0.173 (sired by males other than the paired male breeder, including both within-group and extra-group males) (Townsend et al. 2009)
Carrion Crow	*Corvus corone*	Male and female (Baglione et al. 2002)	0.606 (Canestrari, Marcos, and Baglione 2005)	Yes, but only immigrant helpers (of both sexes) (Baglione et al. 2002)	Unknown
Brown Jay	*Cyanocorax morio*	Male and female (Williams 2004)	0.3731 (Williams 2004)	Yes, for males and females (Williams 2004)	0.333 (includes all incidents of multiple paternity, both within-group and extra-group) (Williams 2004)
Laughing Kookaburra*	*Dacelo novaeguineae*	Male and female (Legge and Cockburn 2000)	0.680 (Legge and Cockburn 2000)	No (Legge and Cockburn 2000)	0.008 (only within-group EPP) (Legge and Cockburn 2000)
Merlin	*Falco columbarius*	Male (James and Oliphant 1986)	At least 0.682 (James and Oliphant 1986)	No/unknown (Warkentin et al. 1994)	0 (Warkentin et al. 1994)
Common Moorhen	*Gallinula chloropus*	Male and female (McRae 1996)	0.393 (McRae 1996)	Yes, often for females and sometimes for males	0 (McRae and Burke 1996)
Australian Magpie	*Gymnorhina tibicen*	Male and female (Hughes et al. 2003)	0.4167 (Hughes et al. 2003)	Yes, for females (males may gain extra-group paternity) (Hughes et al. 2003)	0.8140 (only extra-group paternity, no within-group extra-pair paternity) (Hughes et al. 2003)

Common name	Scientific name	Sex of helpers	Proportion of helpers that are male	"Helpers" may gain direct within-group fitness	Extra-group paternity rate
Superb Starling	*Lamprotornis superbus*	Male and female (Rubenstein 2007a)	Unknown	Yes, for both males and females (Rubenstein 2007b)	0.1377 (18/34 EPY sired by within-group males and 16/34 sired by extra-group males) (Rubenstein 2007b)
Purple-crowned Fairy-wren	*Malurus coronatus*	Male and female (Kingma et al. 2009)	0.692 (Kingma et al. 2009)	Yes, for males, but is very rare; females no (Kingma et al. 2009)	0.04405 (Kingma et al. 2009)
Superb Fairy-wren	*Malurus cyaneus*	Male (Mulder et al. 1994)	1.0 (Mulder et al. 1994)	Yes, but rare (9% of within-group paternity)	0.760 (Mulder et al. 1994)
Splendid Fairy-wren	*Malurus splendens*	Male and female (Webster 2004)	0.8627 (Van Bael and Pruett-Jones 2000)	Yes, for males (commonly)	0.420 (Webster 2004)
Noisy Miner*	*Manorina melanocephala*	Male (Poldmaa, Montgomerie, and Boag 1995)	1.0 (Poldmaa, Montgomerie, and Boag 1995)	No (Poldmaa, Montgomerie, and Boag 1995)	0.0589 (Poldmaa, Montgomerie, and Boag 1995)
Bell Miner*	*Manorina melanophrys*	Male and female (Conrad et al. 1998; Wright et al. 2010)	0.960 (Clarke et al. 2002)	No (Conrad et al. 1998)	0.04167 (Conrad et al. 1998)
Acorn Woodpecker*	*Melanerpes formicivorus*	Male and female (Koenig et al. 2000)	0.5449 (Koenig et al. 2000)	No (Haydock, Koenig, and Stanback 2001)	0 (Haydock, Koenig, and Stanback 2001)
White-fronted Bee-eater	*Merops bullockoides*	Male and female (Emlen and Wrege 1988)	0.47 (Emlen and Wrege 1988)	Yes, for females (Emlen and Wrege 1986)	0.05155 (Wrege and Emlen 1987)
Subdesert Mesite	*Monias benschi*	Male and female (Seddon et al. 2005)	Unknown	Yes, for both males and females (Seddon et al. 2005)	0.09091 (2 offspring with extra-group fathers) (Seddon et al. 2005)
Sociable Weaver*	*Philetairus socius*	Male and female(Covas et al. 2006)	0.75 (Covas et al. 2006)	No (Covas et al. 2006)	0 (Covas et al. 2006)

Common name	Scientific name	Sex of helpers	Proportion of helpers that are male	"Helpers" may gain direct within-group fitness	Extra-group paternity rate
Green Woodhoopoe*	*Phoeniculus purpureus*	Male and female (Radford 2004)	0.3929 (J.D. Ligon and S.H. Ligon 1990)	No (Radford 2004)	0 (Radford 2004; Hawn, Radford, and du Plessis 2007)
Red-cockaded Woodpecker*	*Picoides borealis*	Male and female (Walters, Doerr, and Carter 1988)	0.980 (Walters, Doerr, and Carter 1988)	No (Haig, Walters, and Plissner 1994)	0.0125 (Haig, Walters, and Plissner 1994)
Grey-crowned Babbler	*Pomatostomus temporalis*	Male and female (Blackmore and Heinsohn 2007a)	0.620 (Blackmore and Heinsohn 2007a)	Yes, for both males and females (Blackmore and Heinsohn 2007b)	0.2400 (0.04 by helper males and 0.14 by extra-group males) (Blackmore and Heinsohn 2007b)
American Bushtit*	*Psaltriparus minimus*	Male and female (Sloane 1996)	0.8095 (Sloane 1996)	No (Bruce et al. 1996)	0 (Bruce et al. 1996)
White-breasted Thrasher*	*Ramphocinclus brachyurus*	Male and female (Temple, Hoffman, and Amos 2009)	0.588 (Temple, Hoffman, and Amos 2009)	No (Temple, Hoffman, and Amos 2009)	0.07462 (all extra-group) (Temple, Hoffman, and Amos 2009)
White-browed Scrubwren	*Sericornis frontalis*	Male (Whittingham, Dunn, and Magrath 1997)	1.0 (Whittingham, Dunn, and Magrath 1997)	Yes (Whittingham, Dunn, and Magrath 1997)	0.1240 (by extra-group males and by beta males) (Whittingham, Dunn, and Magrath 1997)
Western bluebird*	*Sialia mexicana*	Male (Dickinson, Koenig, and Pitelka 1996)	1.0 (Dickinson, Koenig, and Pitelka 1996)	No (very rare) (Dickinson and Akre 1998)	0.2208 (Ferree and Dickinson 2011)
Apostlebird*	*Struthidea cinerea*	Male and female (Woxvold, Mulder, and Magrath 2006)	0.7692 (Woxvold, Mulder, and Magrath 2006)	No (Woxvold, Mulder, and Magrath 2006; Woxvold and Magrath 2008)	0 (?) (Woxvold, Mulder, and Magrath 2006)
Pied Babbler	*Turdoides bicolor*	Male and female (Ridley and Raihani 2008)	0.2755 (Ridley and Raihani 2008)	Yes, both males and females, rarely (Nelson-Flower et al. 2011)	0 (or very low) (Nelson-Flower et al. 2011)

Common name	Scientific name	Sex of helpers	Proportion of helpers that are male	"Helpers" may gain direct within-group fitness	Extra-group paternity rate
Tasmanian Native Hen	*Tribonyx mortierii*	Male and female (Gibbs et al. 1994)	0.4473 (A.W. Goldizen et al. 2000)	Yes, for both males and females (Gibbs et al. 1994; A.W. Goldizen et al. 2000)	0 (?) (Gibbs et al. 1994)
Arabian Babbler*	*Turdoides squamiceps*	Male and female (Wright, Parker, and Lundy 1999)	Unknown	No (Lundy, Parker, and Zahavi 1998)	0 or very low (Lundy, Parker, and Zahavi 1998)

APPENDIX 2.2

Proof that p, the proportion of young in the focal male's parents' brood are his full siblings, incorporates the possibility that the focal male was sired by an extra-pair male

1. Let p_1 be the fraction of offspring in the focal brood that are sired by the social male.

2. Let p_2 be the fraction of offspring in the focal brood that are sired by an extra-pair male.

3. With probability p_1, the focal male is the offspring of the social male, and values the other offspring as $[(p_1 * r_{full}) + (p_2 * r_h)]$

4. With probability p_2, the focal male is the offspring of the extra-pair male, and values the other offspring as $[(p_2 * r_{full}) + (p_1 * r_h)]$

5. If the focal male cannot assess his own paternity status (within-pair or extra-pair) or the paternity status of his siblings, he will value the offspring in his parents' brood according to the relative likelihood of each scenario.

6. Thus, the focal male's average relatedness to the offspring in his parents' brood is equal to

$\{p_1 * [(p_1 * r_{full}) + (p_2 * r_h)]\} + \{p_2 * [(p_2 * r_{full}) + (p_1 * r_h)]\}$

Substituting $(1 - p_1)$ for p_2, we obtain the average relatedness to the offspring in the parents' brood: $r_{avg} = r_{full} * (1 - 2*p_1 + 2*p_1^2) + r_h * (2*p_1 - 2*p_1^2)$

7. The average proportion of offspring in the nest that are the focal male's full siblings, assuming that he cannot assess his own or siblings' paternity status, is the weighted average of all the possible p values: $p = [p_1^2 + (1 - p_1)^2]$

8. Substituting p into r_{avg}, we obtain $r_{avg} = [p * r_{full}] + [(1 - p) * r_h]$

as found in Equation 1 in the main text.

APPENDIX 2.3

Proof that the threshold *N*-ratio value, $(p + 1) / (2q)$, is always larger when $p > q$ than when $p < q$.

1. When $p > q$, let $q = (p – x)$, where x is a positive number, so that the denominator of the threshold *N*-ratio value is equal to $(2p – 2x)$

2. When $p < q$, let $q = (p + y)$, where y is a positive number, so that the denominator of the threshold *N*-ratio value is equal to $(2p + 2y)$

3. The numerator, $(p + 1)$, is the same in both cases.

4. The denominator is larger when $p < q$ than when $p > q$ because $y > – x$

5. Therefore, the threshold *N*-ratio value is always larger when $p > q$ than when $p < q$

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CHAPTER 3

COMPETITION FOR EXTRA-PAIR PATERNITY AMONG RELATED MALES AND THE EVOLUTION OF PHILOPATRY

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ABSTRACT

Male philopatry may lead to kin neighborhoods in which genetically related males breed in clusters of independent territories. In non-monogamous genetic mating systems, these related males may compete over both extra-pair paternity and breeding vacancies. Using a game theoretic tug-of-war modeling approach, we first examine how the interaction between the costs of competing with relatives for paternity and the potential inclusive fitness benefits of losing paternity to relatives rather than nonrelatives affects extra-pair mating behavior. Second, we determine whether the costs of competition over extra-pair paternity with relatives may oppose the evolution of philopatry. The model predicts that related males do not necessarily gain a higher proportion of extra-pair paternity or a larger share of pooled reproduction than do unrelated males. Instead, the relative heritable quality of a related male strongly influences the proportion of the focal male's brood that he sires, due to selection on the focal male to reduce guarding investment against high-quality, but not low-quality, relatives. The model also predicts that the reduced investments in conflict by competing relatives means that competition between relatives over extra-pair paternity is less costly than conflict between nonrelatives, and thus that the opportunity to engage in this de-escalated competition contributes to rather than opposes the evolution of philopatry. We suggest that inclusive fitness benefits derived from extra-pair mating

interactions among male relatives may help to explain the evolution of kin structure in populations where kin-directed cooperative behaviors are infrequent or nonexistent.

INTRODUCTION

In birds, dispersal from the natal territory is usually female-biased, and males are more commonly philopatric than are females (Greenwood 1980). Male philopatry may lead to associations of kin living on a single territory, such as cooperatively breeding groups with male helpers or cobreeders (Cockburn 1998), but "exploded" kin associations also occur, in which males breed on independent territories and form territory clusters based on genetic relatedness (Piertney et al. 1999; MacColl et al. 2000; Double et al. 2005; Ribeiro et al. 2012). Similar patterns occur among females in female-philopatric species (McKinnon, Gilchrist, and Scribner 2006; Waldeck et al. 2007). These clusters of related individuals breeding on independent territories are termed "kin neighborhoods" (Dickinson and Hatchwell 2004).

A wide variety of ecological factors, including the availability of suitable habitat and environmental variability, may contribute to selection for philopatry and thus foster the formation of kin associations (Emlen 1982; Koenig et al. 1992). Behavioral factors may also contribute to selection for philopatry: for example, breeding near kin enables males to gain benefits such as access to mates and higher-quality territories (Kraaijeveld and Dickinson 2001) or reduced territorial aggression (Watson et al. 1994; Mougeot et al. 2005), and facilitates opportunistic cooperative behaviors such as redirected helping or joint territory defense (Emlen and Wrege 1988; Dickinson, Koenig, and Pitelka 1996; Hatchwell and Russell 1996; Chapter 4). However, natal philopatry may also result in costly competition among kin. First, competition

may occur over resources such as breeding vacancies (Hamilton and May 1977; Clutton-Brock 2002; Ridley and Sutherland 2002; West, Pen, and Griffin 2002). Second, due to the prevalence of extra-pair mating across bird species (Griffith, Owens, and Thuman 2002), neighboring male kin may compete for paternity of broods after they have gained breeding status. Incorporating extra-pair paternity gains and losses into assessments of males' fitness may significantly alter fitness estimates based on the apparent pedigree derived from banding, indicating that this behavior affects male fitness in important ways (Webster et al. 1995; Ketterson et al. 1998; Richardson and Burke 2001). However, little attention to date has been paid to assessing extra-pair paternity among independently breeding males in a kin neighborhood context (Huyvaert and Parker 2010).

Inclusive fitness analysis (Hamilton 1964a; Hamilton 1964b) indicates that both increased tolerance of paternity loss to relatives over nonrelatives and stealing paternity from relatives may be favored under some conditions (Appendix 3.1). Focusing on the interaction between an independently breeding father and son, a son gains highest inclusive fitness by protecting his own paternity but, if he will inevitably lose paternity, his inclusive fitness is higher if he loses to his father rather than a nonrelative. A father gains highest inclusive fitness by siring extra-pair young in a nonrelative's brood while his son maintains complete paternity but, if he will gain no extra-pair paternity if he does not sire young in his son's brood, he gains higher inclusive fitness by doing so than by avoiding siring young in his son's brood. In this example, both a son's likelihood of losing extra-pair paternity and a father's likelihood of gaining extra-pair paternity influence their competitive interactions with each other. However, this simple comparison does not take into consideration the effect on conflict outcomes of potentially decreased investment in

competition among relatives as compared to nonrelatives (Reeve, Emlen, and Keller 1998). For example, sons may be selected to decrease guarding effort against fathers, further decreasing the costs to fathers of seeking extra-pair copulations with sons' mates. Additionally, the comparative qualities of competing relatives may affect the optimal investments in competition over reproduction: Johnstone (2008) predicted that within-group reproduction will be skewed towards the relative with higher expected fecundity. An inclusive fitness approach in which investment in competition is allowed to vary in response to both relatedness and relative quality is thus more likely to capture the complexity of conflict over extra-pair reproduction.

The two major questions we address here are as follows. First, how does genetic relatedness among breeding males affect extra-pair mating behavior in kin-structured populations? We address this question by examining the extent to which males are selected to reduce mate-guarding effort, effectively forfeiting some proportion of paternity, when interacting with nonrelatives versus relatives of varying heritable genetic quality. Second, does competition with relatives over extra-pair paternity constitute a cost that opposes the evolution of male philopatry? Because losing paternity to an extra-pair male reduces a male's personal fitness, males may be selected to avoid inflicting this cost on relatives by dispersing rather than settling near relatives in populations with competition over extra-pair paternity. We address this question by comparing the inclusive fitness consequences of philopatry and dispersal, considering associations of relatives with both asymmetrical and symmetrical relatedness and identifying the conditions under which conflict over settlement decisions may arise.

The effect of relatedness on extra-pair mating behavior

Two previously developed theoretical frameworks are relevant to this question. The first of these is the evolution of conspecific brood parasitism (CBP). This behavior, in which parasitic females lay eggs in host females' nests, is analogous in function to extra-pair paternity. The observations that waterfowl (Anseriformes) have a higher frequency of CBP than other avian groups (Eadie, Sherman, and Semel 1998) and also exhibit a dispersal pattern opposite to that of most birds (dispersal is male-biased and females tend to be philopatric) may be explained by kin selection acting on philopatric females that accept parasitic eggs from relatives (Hamilton 1964a; Hamilton 1964b; Andersson 1984; McRae and Burke 1996). Mathematical models predict that the frequency of CBP relative to solitary or cooperative breeding may decrease with increasing relatedness between parasite and host, due to the inclusive fitness costs a parasitic female suffers by inflicting the costs of parasitism on a relative (Zink 2000), or increase due to the inclusive fitness costs a host female suffers when she resists parasitism by a relative (Andersson 2001). However, we know of no investigations to date of how the inclusive fitness benefits of being parasitized by relatives may contribute to the evolution of female philopatry.

The second relevant framework is reproductive skew theory, which was developed to examine the conditions affecting the degree of inequality in reproductive partitioning among group members (Vehrencamp 1983; Reeve and Ratnieks 1993; Keller and Reeve 1994; Reeve, Emlen, and Keller 1998). This framework is relevant because we view individuals breeding on independent territories in kin neighborhoods as "exploded" family groups. Where extra-pair paternity occurs, related, but independently breeding, males potentially compete for paternity of offspring. Thus we can examine how partitioning of paternity across broods differs between

relatives and nonrelatives. Existing skew models predict that relatedness among competing group members may increase the inequality in reproductive partitioning among competitors when one individual has complete control over reproduction (Vehrencamp 1983) and have no effect on skew when neither individual has complete control (Reeve, Emlen, and Keller 1998; Shen and Reeve 2010). In an important advance, a tug-of-war model incorporating local competition predicted that philopatry, and hence increased local relatedness, will result in increased within-group reproductive skew, with the individual having higher expected fecundity gaining a larger share of reproduction (Johnstone 2008). However, the model did not consider the partitioning of reproduction across kin neighborhoods in which individuals breed independently.

The effect of kin extra-pair mating competition on philopatry

To our knowledge, no theoretical or empirical investigations have focused on the extent to which kin competition over extra-pair paternity may affect the evolution of male philopatry. However, theoretical work suggests that kin competition can contribute to the evolution of dispersal by increasing the costs of philopatry (Hamilton and May 1977) even when dispersers also incur fitness costs (Perrin and Lehmann 2001). This prediction is supported by empirical work indicating that dispersers facing kin competition will leave the natal patch under riskier conditions than will dispersers facing intraspecific competition with nonrelatives (Cote and Clobert 2010). Thus, it is plausible that the high fitness costs of competition with relatives for paternity-losing males could oppose selection for male philopatry. On the other hand, if paternity loss is likely due to a high frequency of extra-pair matings, the opportunity to lose paternity to relatives rather than non-relatives may be an important benefit for male birds, and thus may contribute to selection for philopatric settlement. It is important to note that many factors may

affect the costs and benefits of philopatry; for example, habitat saturation leading to low availability of breeding territories may increase the benefits of philopatry (Brown 1974). The relative importance of these factors likely varies among species (Koenig et al. 1992). Here, we examine the contribution of kin paternity competition to selection on philopatry, holding all other potentially contributing ecological and behavioral factors equal.

Modeling interactions in kin associations

We use a game theoretic "tug-of-war" modeling approach (Reeve, Emlen, and Keller 1998) to examine the relationship between genetic relatedness among breeding males and extra-pair mating competition in kin-structured populations; the key features of our approach are summarized in Table 3.1. We ask (1) how relatedness and heritable genetic quality influence patterns of extra-pair mating and reproductive skew between independently breeding males, and (2) how competition between male kin over extra-pair paternity influences selection for philopatry versus dispersal. We assume that neither of two males has complete control over reproduction but instead each invests energy in both guarding his own mate and attempting to gain extra-pair paternity in the other male's brood. We allow heritable genetic quality (meaning the individual's "breeding value for total fitness"; c.f. Hunt et al. 2004) to vary between the males, incorporating potential age-based variation in male quality (Kokko 1998; Brooks and Kemp 2001). Our major results are as follows. First, the model predicts that relatedness alone does not affect extra-pair paternity or reproductive skew, but instead combines with the effects of heritable genetic quality on these parameters. Among related males, the male with higher heritable genetic quality gains a higher proportion of extra-pair paternity, and skew increases with the disparity in heritable genetic quality between the males. Among unrelated males,

heritable genetic quality does not influence extra-pair paternity or skew. Second, the model predicts that kin competition over extra-pair paternity is not sufficiently costly to disfavor the evolution of male philopatry. Instead, the fitness benefits of reduced competition among relatives versus nonrelatives contribute to selection for philopatry.

Table 3.1 Important features and assumptions of the model.

1. The conflict is modeled as a tug-of-war
2. The conflict is modeled as a two-player interaction
3. We assume conservation of paternity: all offspring are sired by either Male 1 or Male 2
4. We assume a tradeoff between effort invested in conflict (guarding, attempting to gain extra-pair copulations) and parental investment
5. Males are allowed to vary in heritable genetic quality (v)
6. Males are allowed to vary in competitive efficiency, which captures their relative ability to capitalize on opportunities to gain extra-pair copulations. This term captures the likelihood that a female will accept the male as an extra-pair mate, or his "desirability" as an extra-pair mate, as well as disparities in extra-pair copulation success due to experience
7. Females do not participate directly in the conflict
8. Males have equal mate-guarding efficiencies
9. Sons do not seek extra-pair copulations with mothers (incest avoidance).

THE MODEL

Consider two males, each of which possesses a brood for which he provides care, in cooperation with his mate. These males interact with each other's mates such that each male may sire extra-pair offspring in the other's brood. We assumed that the females do not invest in conflict over extra-pair paternity at the expense of parental investment, an assumption that is supported under a biologically realistic range of parameters (Chapter 1). The proportion of offspring in Brood 1 (the brood cared for by Male 1) that are sired by Male 2 is denoted epp_1 and, in accordance with tug-of-war theory (Reeve, Emlen, and Keller 1998), is determined by Male 2's investment in gaining EPP (x_2) relative to the sum of that investment and Male 1's investment in protecting his own paternity (y_1):

$$epp_1 = \frac{x_2}{x_2 + y_1} \tag{1}$$

Similarly, the proportion of offspring in Brood 2 (the brood cared for by Male 2) that are sired by Male 1 is denoted epp_2 and is determined by Male 1's investment in gaining EPP (x_1) relative to the sum of that investment and Male 2's investment in protecting his own paternity (y_2). However, Male 1's investment in gaining EPP is devalued by b, his competitive efficiency relative to Male 2:

$$epp_2 = \frac{(b * x_1)}{(b * x_1) + y_2} \tag{2}$$

This competitive efficiency term represents Male 1's relative ability to convert investment in gaining EPP into actual EPP gains, e.g. due to his experience with seeking extra-pair mating opportunities (Weatherhead and Boag 1995) or his attractiveness to extra-pair females, and ranges from greater than zero to less than or equal to one (Table 3.2). This term differs from the traditional b term in tug-of-war models (Reeve, Emlen, and Keller 1998) in that it is not

interpreted as the focal male's physical fighting ability. We assumed that males 1 and 2 have equal ability to defend their own paternity, an assumption that could be relaxed by multiplying investment y_1 in Equation 1 by a separate competitive efficiency term. Also note that paternity conservation is complete: all offspring are sired by either Male 1 or Male 2 (Houston and McNamara 2002). This assumption is important because it makes the model self-consistent, and justified because multiple extra-pair sires are relatively rare across studied species (Chapter 1). However, expanding the model to include more than two interacting males, while maintaining self-consistency through paternity conservation, is an important future goal.

We captured the cost of investing in conflict by incorporating a tradeoff between investment in conflict and investment in brood care: each male's conflict investments are subtracted from the total energy he has available for parental investment, which we set equal to 1 for convenience. Incorporating the female's parental investment, which we set equal to 1 (assuming that females are not selected to invest in conflict over EPP at the expense of parental investment), the total parental investments in Broods 1 and 2, respectively, are equal to

$$brood_1 = (1 - x_1 - y_1) + (1) \quad (3)$$

and

$$brood_2 = (1 - x_2 - y_2) + (1) \quad (4)$$

Thus, Male 1's total fitness derived through direct reproduction in his own brood is equal to

$$r_1 * (1 - epp_1) * brood_1 \quad (5)$$

and Male 1's total fitness derived through direct reproduction in Male 2's brood is equal to

$$r_1 * (epp_2) * brood_2 \quad (6)$$

where Male 1's coefficient of relatedness with his own offspring is equal to r_1.

Table 3.2 Variables used in the model.

Variable	Definition	Possible values
x_1	Male 1's investment in gaining extra-pair paternity (EPP) in Male 2's brood (Brood 2)	$0 \le x_1 \le 1; x_1 + y_1 \le 1$
y_1	Male 1's investment in thwarting Male 2's attempts to gain EPP in Male 1's brood (Brood 1)	$0 \le y_1 \le 1; x_1 + y_1 \le 1$
x_2	Male 2's investment in gaining EPP in Brood 1	$0 \le x_2 \le 1; x_2 + y_2 \le 1$
y_2	Male 2's investment in thwarting Male 1's attempts to gain EPP in Brood 2	$0 \le y_2 \le 1; x_2 + y_2 \le 1$
r_1	Male 1's coefficient of genetic relatedness with his offspring	$0 \le r_1 \le 1$
r_2	Male 2's coefficient of genetic relatedness with his offspring	$0 \le r_2 \le 1$
r_{121}	Male 1's coefficient of genetic relatedness with Male 2's within-pair offspring	$0 \le r_{121} \le 1$
r_{122}	Male 1's coefficient of genetic relatedness with Male 2's extra-pair offspring	$0 \le r_{122} \le 1$
r_{21}	Male 2's coefficient of genetic relatedness with Male 1's offspring	$0 \le r_{21} \le 1$
b	Male 1's competitive efficiency relative to Male 2	$0 \le b \le 1$
v	Male 2's heritable genetic quality relative to Male 1	$0.5 < v < 2$*

*Other v values are possible, but we used this range for biologically realism.

Similarly, Male 2's total fitness derived through direct reproduction in his own brood, and his total fitness derived through direct reproduction in Male1's brood, are equal to

$$r_2 * (1 - epp_2) * brood_2 \quad (7)$$

and

$$r_2 * (epp_1) * brood_1 \quad (8)$$

respectively, where Male 2's coefficient of relatedness with his own offspring is equal to r_2.

Using the terms from Equations 5-8, we constructed the inclusive fitness functions for males 1 and 2 as follows:

$$IF_1 = (r_1 * \{[(1 - epp_1) * brood_1] + [epp_2 * brood_2]\}) + (r_{12} * \{[(1 - epp_2) * brood_2] + [epp_1 * brood_1]\}) \quad (9)$$

$$IF_2 = (r_2 * \{[(1 - epp_2) * brood_2] + [epp_1 * brood_1]\}) + (r_{21} * \{[(1 - epp_1) * brood_1] + [epp_2 * brood_2]\}) \quad (10)$$

Here, Male 1's coefficient of relatedness with Male 2's offspring is equal to r_{12}, and Male 2's coefficient of relatedness with Male 1's offspring is equal to r_{21}. All variables used in the model are summarized in Table 3.2.

Heritable genetic quality

Difference in heritable genetic quality between son and father or son and stepfather could affect the evolutionary outcome of the competition. For example, because fathers are older than sons, their average genetic quality may exceed that of sons because fathers will have experienced stronger prior selection for high viability genes (Kokko and Lindstrom 1996; Kokko 1998). We allowed for this possibility by incorporating a heritable genetic quality term (v), which captures

the heritable genetic quality of Male 2 relative to Male 1. This term appears in the fitness functions as follows:

$$IF_1 = (r_1 * \{[(1 - epp_1) * brood_1] + [epp_2 * brood_2]\}) + (r_{12} * v * \{[(1 - epp_2) * brood_2] + [epp_1 * brood_1]\} \quad (11)$$

$$IF_2 = (r_2 * v * \{[(1 - epp_2) * brood_2] + [epp_1 * brood_1]\}) + (r_{21} * \{[(1 - epp_1) * brood_1] + [epp_2 * brood_2]\}) \quad (12)$$

Incest avoidance

When Male 2's mate is Male 1's mother, we assumed that Male 1 will avoid incest by refraining from seeking extra-pair copulations with his mother. However, Male 2 may still seek extra-pair copulations with Male 1's mate, and Male 1 may still invest in guarding his mate. Thus, we reformulated the model to include y_1 and x_2 but not x_1 and y_2 in the incest avoidance case:

$$epp_1 = \frac{x_2}{x_2 + y_1} \quad (13)$$

$$brood_1 = (1 - y_1) + (1) \quad (14)$$

$$brood_2 = (1 - x_2) + (1) \quad (15)$$

$$IF_1 = [r_1 * (1 - epp_1) * brood_1] + \{v * [(r_{121} * brood_2) + (r_{122} * epp_1 * brood_1)]\} \quad (16)$$

$$IF_2 = \{r_2 * v * [brood_2 + (epp_1 * brood_1)]\} + [r_{21} * (1 - epp_1) * brood_1] \quad (17)$$

Here, Male 1's coefficient of relatedness with Male 2's within-pair offspring is equal to r_{121}, Male 1's coefficient of relatedness with Male 2's extra-pair offspring is equal to r_{122}, and Male

2's coefficient of relatedness with Male 1's offspring is equal to r_{21}. Note that, because Male 1 does not seek extra-pair copulations with his mother, these functions do not include Male 1's competitive efficiency relative to Male 2 (b).

Solving the model

To find each male's evolutionarily stable (Maynard Smith 1974) investments in conflict, we took the partial derivative of each fitness function with respect to the appropriate male's decision variable; e.g., for the case in which the males are full brothers we took the partial derivatives $\partial x_1/\partial IF_1$, $\partial y_1/\partial IF_1$, $\partial x_2/\partial IF_2$, and $\partial y_2/\partial IF_2$. We solved the model numerically by specifying values for the appropriate parameters (e.g., v, r_1, r_{121}, r_{122}, r_2, and r_{21} for the case in which Male 2 is Male 1's stepfather) then solving for the values of the decision variables at which all the partial derivatives are equal to zero. We confirmed that our solutions represent endpoint maxima using the second derivative test. Throughout, we assumed that individuals are diplo-diploid and that the behaviors in questions are encoded by unimprinted, autosomal alleles (Haig 2000). The four cases we examined here, along with the sets of r values we used in our numerical solutions, are 1) full brothers ($r_1 = 0.5, r_{121} = r_{122} = 0.25, r_2 = 0.5, r_{21} = 0.25$); 2) son-father, where the father is mated to a step-mother ($r_1 = 0.5, r_{121} = r_{122} = 0.25, r_2 = 0.5, r_{21} = 0.25$); 3) non-relatives ($r_1 = 0.5, r_{121} = r_{122} = 0, r_2 = 0.5, r_{21} = 0$); 4) son-stepfather, where the stepfather is mated to the focal male's mother ($r_1 = 0.5, r_{121} = 0.25, r_{122} = 0, r_2 = 0.5, r_{21} = 0$); and 5) son-father, where the father is mated to the focal male's mother ($r_1 = 0.5, r_{121} = 0.5, r_{122} = 0.25, r_2 = 0.5, r_{21} = 0.25$). Note that relatedness is symmetrical in cases 1-3 and asymmetrical in cases 4-5, which also incorporate incest avoidance. The term "father" above indicates the genetic father; we assume that the father is the genetic father for simplicity. It is appropriate to use the relatedness value for genetic father-son if sons are able to assess their own paternity status (i.e., whether they are extra-pair

and should behave towards their social father as towards a step-father, or if they are within-pair). However, if sons instead behave in accordance with average social father-son relatedness in the population, the appropriate value may be less than one-half. Investigating the effects of decreased average social father-son relatedness on the model outcomes is an important avenue for future research. We used the program Mathematica 8.0 for all model analyses (Wolfram Research, Inc.; Champaign, IL; U.S.A.).

Evaluating inclusive fitness

The model allows us to infer the focal male's optimal settlement decision (philopatry or dispersal) by comparing the inclusive fitness he gains in each interaction. We assumed that conflict participation is determined spatially, meaning that males engaged in conflict over paternity are near, though not necessarily nearest, neighbors. We also assumed that the focal male will settle on a breeding territory either near a relative, a situation we term philopatry, or near a nonrelative, which we term dispersal (Table 3.3). We examined the effects of dispersal under low and high density. In the low density condition, the focal male's dispersal results in his male relative breeding in isolation, meaning that the male relative neither gains extra-pair paternity nor loses within-pair paternity. In the high density condition, the vacancy unfilled by the focal male is filled by another male, such that the focal male's relative breeds near a nonrelative. For each case, we calculated the focal male's inclusive fitness using the numerical solutions generated through solving the model; the inclusive fitness functions are displayed in Table 3.4. Because the focal male's competitive efficiency did not qualitatively affect the predictions in the asymmetrical relatedness cases, all results we show for those cases are for $b = 1$. We also calculated the inclusive fitness of the focal male's rival (his father, stepfather, or brother) in each case in order to identify potential zones of conflict over settlement decisions.

Table 3.3 The interactions across which we compared inclusive fitness outcomes.

Case	Male A	Male A's rival	Male B	Male B's rival
1. Philopatry	Focal male	Relative	---	---
2. Dispersal – low density	Focal male	Nonrelative	Relative	---
3. Dispersal – high density	Focal male	Nonrelative	Relative	Nonrelative

Table 3.4 The functions used in calculating the inclusive fitness consequences of philopatry versus dispersal for the focal male.

Case[1]	Interacting pair	Focal male's inclusive fitness
(1)	Father and mother OR Stepfather and mother	$[r_1 * (1 - epp_1) * brood_1] + \{v * [(r_{121} * brood_2) + (r_{122} * epp_1 * brood_1)]\}$
(2)	Father and mother OR Stepfather and mother	$(r_1 * \{[(1 - epp_1) * brood_1] + [epp_2 * brood_2]\}) + (2 * v * r_{121})$
(3)	Father and mother OR Stepfather and mother	$(r_1 * \{[(1 - epp_1) * brood_1] + [epp_2 * brood_2]\}) + (1 * v * r_{121})$
(1)	Related male and unrelated female[2]	$(r_1 * \{[(1 - epp_1) * brood_1] + [epp_2 * brood_2]\}) + (r_{12} * v * \{[(1 - epp_2) * brood_2] + [epp_1 * brood_1]\}$
(2)	Related male and unrelated female	$(r_1 * \{[(1 - epp_1) * brood_1] + [epp_2 * brood_2]\}) + (2 * v * r_{121})$
(3)	Related male and unrelated female	$(r_1 * \{[(1 - epp_1) * brood_1] + [epp_2 * brood_2]\}) + (1 * v * r_{121})$

[1]See Table 3.3 for definitions of the numbered cases

[2]The related male is either the focal male's full brother or father. For same-age brothers, $v = 1$.

RESULTS

Extra-pair paternity allocation and reproductive skew across independent broods

Here, we define reproductive skew as the proportion of offspring sired by the non-focal male across both broods. Thus, reproductive skew equal to 0.5 corresponds to equitable division of reproduction between the males. Skew values less than 0.5 indicate that the focal male gains a larger share of reproduction than does the non-focal male, while skew values greater than 0.5 indicate the reverse.

First, we compared a focal male interacting with his mother and father to a focal male interacting with his mother and stepfather (both cases with asymmetrical relatedness). We assumed that the male will not attempt to copulate with his mother (incest avoidance), but that his mother's mate may attempt to gain paternity in the focal male's brood. Thus, the father or stepfather has complete paternity in his own brood, but the focal male may lose some fraction of paternity. The model predicts that the focal male is selected to invest at least double the energy in protecting his within-brood paternity against his stepfather than against his father (Figure 3.1). The focal male's guarding effort is unresponsive to his stepfather's relative heritable genetic quality and remains consistently high, but declines to near zero when his father's heritable genetic quality is high (Figure 3.1). This reduced guarding by the focal male when the father's reproductive value is greater than approximately 0.8 results in a father gaining a larger proportion of the focal male's paternity than does a stepfather, whose proportion of paternity gained is unresponsive to his relative heritable genetic quality (Figure 3.2). Following on these patterns, the model predicts that reproductive skew is higher in son-father than in son-stepfather associations when the father's heritable genetic quality is greater than approximately 0.8 (Figure 3.3).

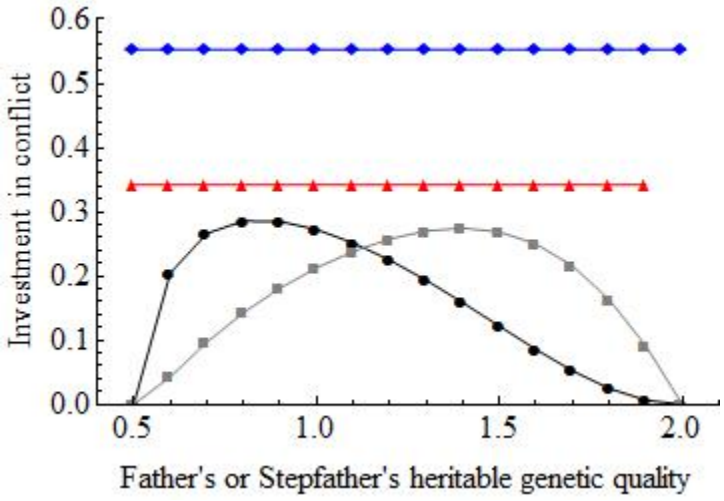

Figure 3.1 Investment in guarding behavior by a focal male interacting with his father (black circles) or his stepfather (blue diamonds) in the face of investment in extra-pair paternity seeking behavior by his father (gray squares) or stepfather (red triangles). Investments in conflict are higher in the son-stepfather case than in the son-father case.

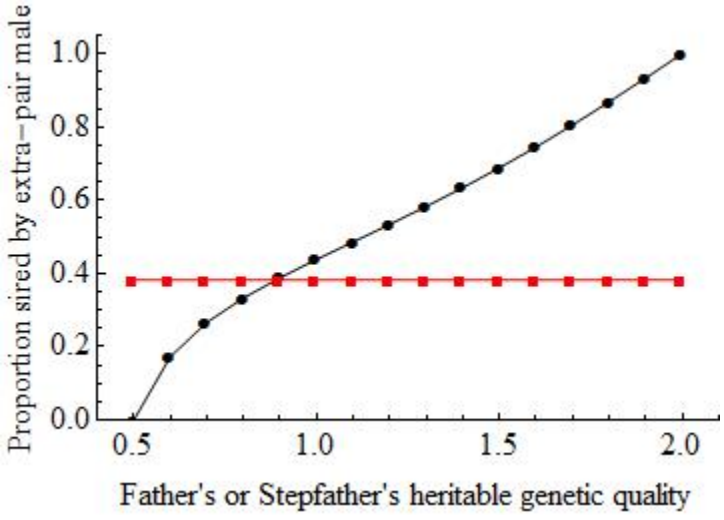

Figure 3.2 The proportion of the focal male's brood that is sired by his father (black circles) or stepfather (red squares) in relation to the father or stepfather's relative heritable genetic quality

(*v*). A father gains a higher proportion of paternity in his son's brood than does a stepfather when *v* is greater than approximately 0.8.

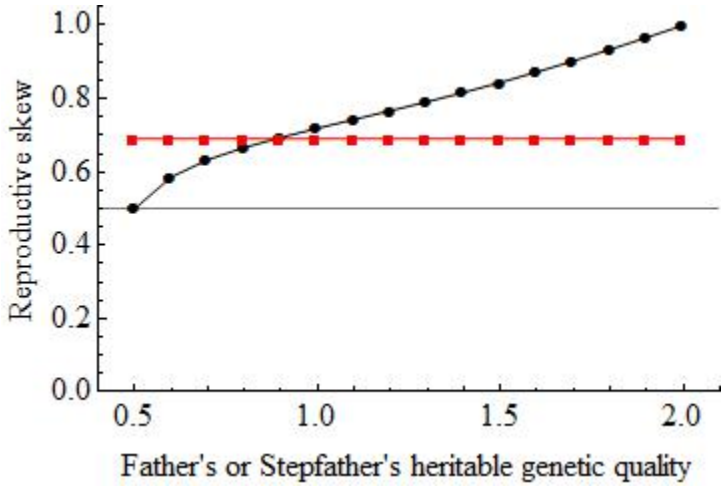

Figure 3.3 The proportion of offspring across both broods that are sired by a focal male's father (black circles) or stepfather (red squares) in relation to the father's or stepfather's relative heritable genetic quality (*v*). The horizontal line at reproductive skew = 0.5 represents equitable division of reproduction between the two males. Skew is higher when a son interacts with his father than with his stepfather when *v* is greater than approximately 0.8; thus, the model predicts that reproductive skew will be higher in son-father than in son-stepfather associations when the father's heritable genetic quality is equal to or greater than his son's.

Second, we compared a focal male's interactions with two types of symmetrically related males: a relative mated to an unrelated female (either a full brother mated to an unrelated female or a father mated to a stepmother), and a non-relative mated to an unrelated female. The model predicts that the focal male's investment in guarding his within-brood paternity is consistently highest when interacting with a non-relative (Figure 3.4). Among the relative-relative

interactions we examined, the focal male's guarding effort is highest when he is interacting with a full brother or father of equal heritable genetic quality. The proportion of extra-pair offspring in the focal male's brood (i.e., the focal male's within-brood paternity loss) is not determined by relatedness alone (Figure 3.5): while a relative's heritable genetic quality affects the proportion of extra-pair offspring he sires, the proportion of extra-pair offspring relatives are predicted to sire ranges from close to zero to close to one, entirely encompassing the predicted range of proportions for non-relatives. The model predicts that reproduction is equitably divided when the focal male's competitive efficiency is equal to the second male's and 1) the second male is a non-relative, or 2) the second male is a relative with equal heritable genetic quality (e.g., same-age brothers) (Figure 3.6). As the focal male's competitive efficiency decreases relative to the second male's, reproduction becomes increasingly skewed towards the second male. Among relatives, skew also varies with heritable genetic quality such that reproduction is skewed towards related rivals with high heritable genetic quality and away from related rivals with low heritable genetic quality, the focal male's competitive efficiency being held equal (Figure 3.6).

Overall, the model predicts that relatedness will have a stronger effect on reproductive partitioning in associations of asymmetrically related males than symmetrically related males. When his father's heritable genetic quality is equal to or greater than his own, as we would expect usually to be the case, the focal male's guarding effort and the extra-pair copulation-seeking effort of his rival interact such the male's father gains a higher proportion of paternity in the male's brood than does the male's stepfather. Heritable genetic quality also importantly influences reproductive skew among symmetrically related males: the male with greater relative heritable genetic quality will gain a larger proportion of reproduction when males are related.

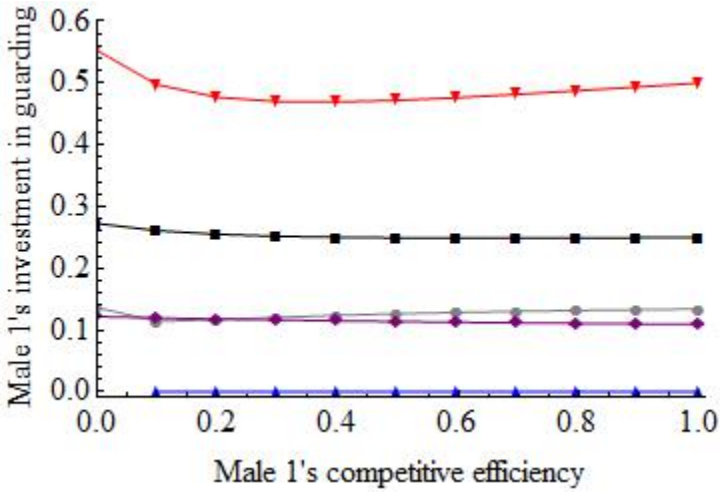

Figure 3.4 The focal male's investment in guarding his within-brood paternity is consistently higher when interacting with a non-relative. The interactions displayed are those of the focal male with 1) a non-relative (red, down-pointing triangles); 2) his brother, or his father where his father has heritable genetic quality equal to his own (black squares); 3) his father where his father's relative heritable genetic quality = 0.55 (gray circles); 4) his father where his father's relative heritable genetic quality = 1.5 (purple diamonds); and 5) his father where his father's relative heritable genetic quality = 1.99 (blue, up-pointing triangles). Note that, for all interactions between the focal male and his father, the father is mated to a female unrelated to the focal male (his stepmother).

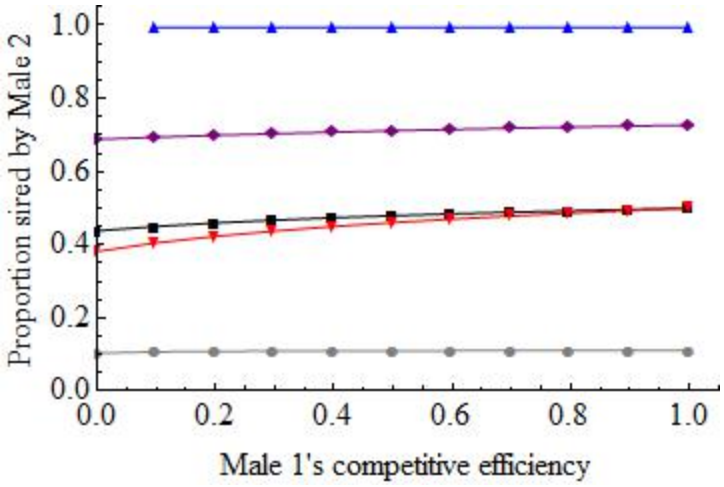

Figure 3.5 The proportion of extra-pair offspring in the focal male's brood is unaffected by relatedness: similar proportions are predicted for interactions with both related and unrelated males. See Figure 3.4 caption for legend.

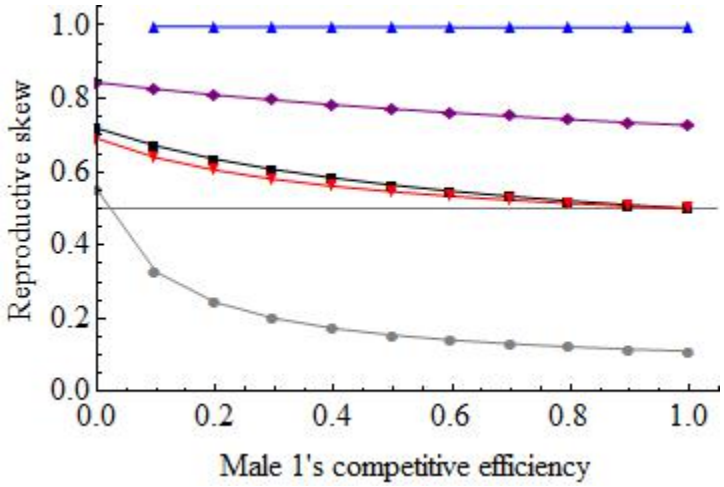

Figure 3.6 The proportion of offspring across both broods that are sired by a focal male's opponent. The horizontal line at reproductive skew = 0.5 represents equitable division of reproduction between the two males. See Figure 3.4 caption for legend. Note that, for all interactions between the focal male and his father, the father is mated to a female unrelated to the focal male (his stepmother).

Inclusive fitness consequences of philopatry versus dispersal

Under asymmetrical relatedness and incest avoidance, the focal male's inclusive fitness is maximized when he is philopatric and interacting with his father and mother (Figure 3.7). Interestingly, philopatry is not the fitness maximizing option when the focal male is determining whether to settle near his stepfather and mother or disperse: in this case, dispersal under low density yields higher inclusive fitness. For both types of asymmetric interactions, however, dispersal under high density yields the lowest inclusive fitness (Figure 3.7). Thus, the model predicts that if competition for territories is sufficient to ensure that any vacancy left unfilled by the focal male will be filled by a nonrelative, the focal male is selected to breed in philopatry near his father and mother or stepfather and mother. An important contributor to this pattern is the fitness benefits of the decreased investments in conflict among relatives: when relatives interact, each invests less energy in conflict, thus reaping both the direct fitness benefits of increased parental investment and the indirect fitness benefits of increased parental investment by relatives.

Under symmetrical relatedness, the focal male's inclusive fitness is maximized when he is philopatric (Figure 3.8). This pattern holds for all v values we tried, including in the case of same-age brothers ($v = 1$). Dispersal at low density yields intermediate inclusive fitness values, while dispersal at high density corresponds to the lowest inclusive fitness values.

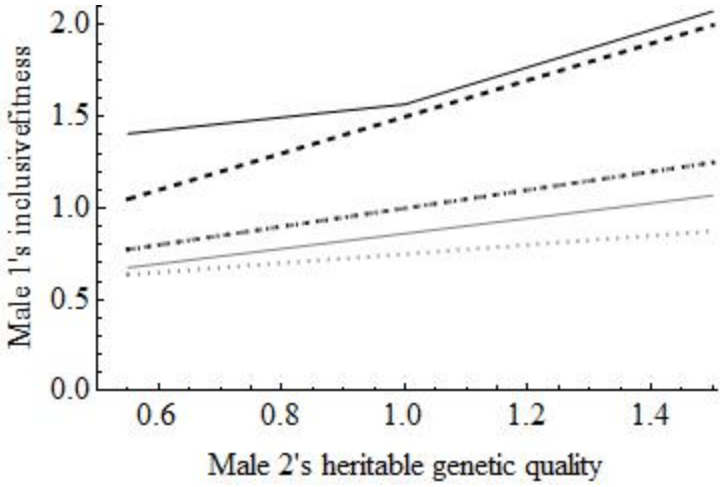

Figure 3.7 Under asymmetrical relatedness, the focal male's inclusive fitness is maximized when he breeds near his father and mother. For both types of asymmetric interactions, philopatry (solid lines) yields higher inclusive fitness than dispersal under high density (dotted lines). Black lines correspond to interactions with a father and mother, while gray lines correspond to interactions with a stepfather and mother. Dashed lines indicate dispersal under low density.

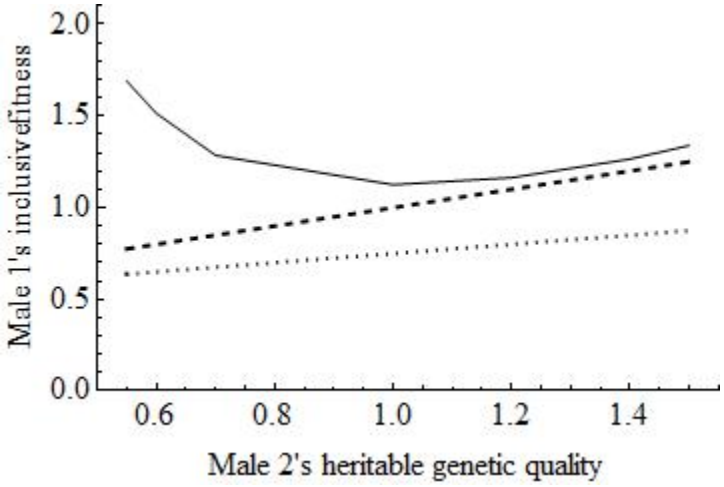

Figure 3.8 Under symmetrical relatedness, the focal male's inclusive fitness is maximized when he is philopatric (solid line), including in the case of same-age brothers ($v = 1$). Dispersal at low density (dashed line) yields higher inclusive fitness than dispersal at high density (dotted line).

We compared the inclusive fitness of the focal male's rival (father, stepfather, or brother) with the focal male's inclusive fitness to identify conditions under which conflict over settlement decisions may occur. Under asymmetrical relatedness, whether the second male is the focal male's father or his stepfather, the second male's inclusive fitness is maximized when the focal male is philopatric and minimized when the focal male disperses under high density (Figure 3.9). Thus, the inclusive fitness interests of the focal male and his father are aligned with respect to the rankings of the three options: both have highest inclusive fitness when the focal male is philopatric, and lowest when he disperses under high density. However, the inclusive fitness interests of the focal male and his stepfather are not aligned: the focal male has highest inclusive fitness when he disperses under low density, while the stepfather has highest inclusive fitness when the focal male is philopatric, suggesting the potential for settlement conflict.

Under symmetrical relatedness, the second male's inclusive fitness is maximized when the focal male is philopatric only for low or high values of relative heritable genetic quality (v < approx. 0.7 and v > approx. 1.3) (Figure 3.10). For the middle range of heritable genetic quality values, the second male's inclusive fitness is maximized when the focal male disperses under low density. Because the focal male's inclusive fitness is maximized under philopatry, the degree to which the males' inclusive fitness interests are aligned depends upon the second male's heritable genetic quality. However, the second male's inclusive fitness is higher when the focal male is philopatric than when the focal male disperses under high density, a relevant comparison if dispersal under low density is not an available option, and in that case the inclusive fitness interests of the males are aligned.

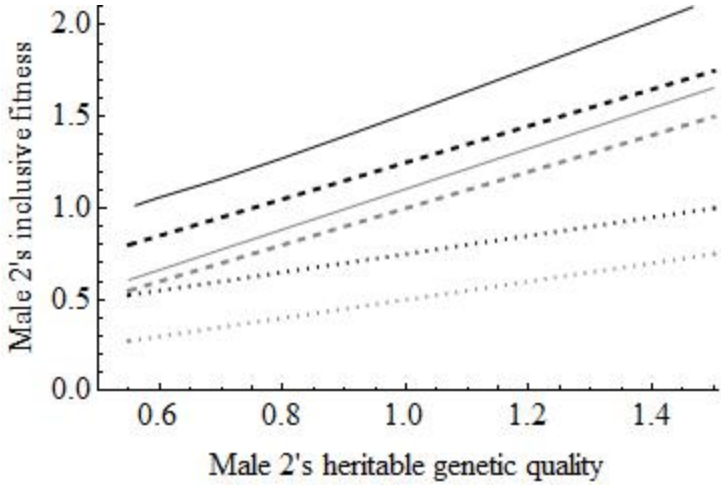

Figure 3.9 Under asymmetrical relatedness, whether the second male is the focal male's father (black lines) or his stepfather (gray lines), the second male's inclusive fitness is maximized when the focal male is philopatric (solid lines) and minimized when the focal male disperses under high density (dotted lines). Dashed lines indicate dispersal under low density.

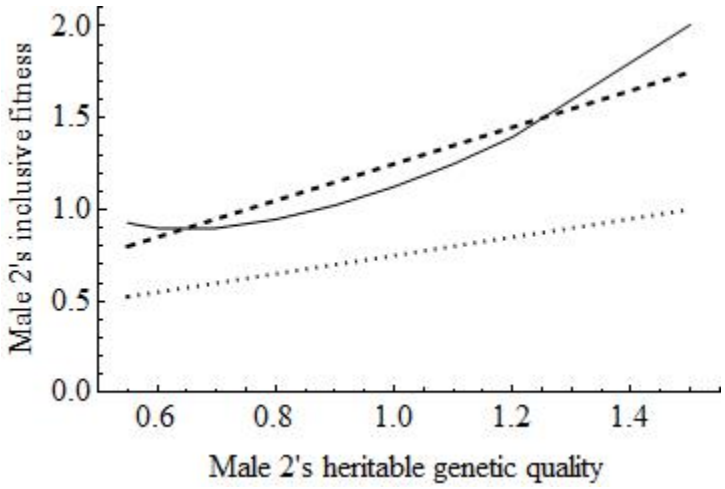

Figure 3.10 In a high-density population, the symmetrically-related second male's inclusive fitness is higher when the focal male is philopatric (solid line) than when the focal male disperses (dotted line). The dashed line indicates dispersal under low density.

DISCUSSION

Briefly, the model predicts that related males do not necessarily gain a higher proportion of extra-pair paternity or a larger share of pooled reproduction than do unrelated males; instead, the relative heritable genetic quality of a rival related male strongly influences the extent to which a focal male is selected to reduce his guarding behavior, thus suffering a reduction in paternity and reproductive share. The model also predicts that, from the perspective of the focal male, the inclusive fitness benefits of competing with relatives rather than nonrelatives over extra-pair paternity contribute to rather than oppose the evolution of philopatry. We discuss these predictions in more detail below.

Extra-pair paternity allocation and reproductive skew across independent broods

The tug-of-war model predicts that males are not necessarily selected to yield a higher proportion of extra-pair paternity to relatives than to nonrelatives. Instead, the proportion of the focal male's brood sired by the rival male varies strongly with the rival's heritable genetic quality, when the rival is a relative. The model predicts that the proportion of paternity gained by related and unrelated males will be equivalent when the related male has heritable genetic quality equal to the focal male. Among related males, the proportion of paternity gained by the non-focal male is predicted to be proportional to his relative heritable genetic quality. This finding accords with previous work suggesting that intrinsic differences such as expected fecundity can importantly influence reproductive competition among relatives (Johnstone 2008). We predict by analogy that the relative heritable genetic qualities of the interacting females may importantly affect selection on both parasite targeting and host acceptance behavior in species exhibiting conspecific brood parasitism. In wood ducks (*Aix sponsa*), hosts may be more likely to accept

parasitic eggs laid by relatives than those laid by nonrelatives (Nielsen et al. 2006), and young females are more likely than older females to lay parasitic eggs (Semel and Sherman 2001). However, the comparative genetic qualities of parasites and hosts in this species are currently unknown. Testing this prediction in the several species in which host-parasite relatedness has been examined (Eadie and Lyon 2011) could reveal interesting parallels between female-female and male-male conflicts over reproductive opportunities.

A related rival's heritable genetic quality also influences reproductive skew across the pooled broods: depending upon the rival's quality, skew may be equivalent between related versus unrelated males. However, reproductive skew becomes more inequitable when males are related than when they are unrelated in both asymmetrically and symmetrically related male dyads. The results are thus partially in accordance with those of a previous tug-of-war model (Johnstone 2008). However, the previous model found that variation in skew with relatedness only occurs when the competing individuals have unequal competitive ability (Johnstone 2008). In contrast, we found that when individuals have equal ability to capitalize on both investment in gaining extra-pair copulations ($b = 1$) and investment in mate guarding (assumed in our model to be equal across males), skew values may still differ among related versus unrelated males depending upon heritable genetic quality. In this scenario, reproduction is skewed towards the related male with higher heritable genetic quality. Reproduction is divided equitably among unrelated males under symmetrical relatedness and biased towards the stepfather under asymmetrical relatedness. Our model thus reveals an important additional effect of heritable genetic quality on reproductive partitioning among relatives, suggesting that the male with lower

heritable genetic quality is selected to reduce investment in guarding against his higher-heritable genetic quality relative.

Among symmetrically related males, the fraction of reproduction the focal male gains increases with his relative competitive efficiency, such that the focal male sires a higher proportion of the young across both broods when he has higher relative competitive efficiency (e.g., is more strongly preferred by females as an extra-pair mate). The presence of this pattern among both relatives and nonrelatives indicates that the effects of competitive efficiency on reproductive skew, unlike those of heritable genetic quality, are not contingent upon relatedness. However, relative competitive ability does not influence reproductive skew when the rival male is mated to the focal male's mother, due to our assumption of incest avoidance.

Inclusive fitness consequences of philopatry versus dispersal

Although kin competition over limited reproductive opportunities may oppose the evolution of philopatry (Hamilton and May 1977; Perrin and Lehmann 2001; Cote and Clobert 2010), our model predicts that kin-selected reductions in competitive investment among relatives in the context of extra-pair mating contribute to the evolution of philopatry. Comparing the options of breeding in philopatry, breeding near a nonrelative while a relative breeds solitarily (neither losing nor gaining extra-pair paternity), or breeding near a nonrelative while a relative does the same reveals that the focal male maximizes his inclusive fitness through philopatry in every case we examined (the interacting pair is father-mother, father-stepmother, or brother-female nonrelative) except when the interacting pair is a stepfather mated to the male's mother. In the latter case, the focal male maximizes his inclusive fitness by dispersing while the related pair breeds solitarily; however, if competition for breeding territories is high enough that the

territorial vacancy will be filled by a nonrelative, philopatry is again the fitness-maximizing option. This result is especially interesting given that superficial examination of parameters such as extra-pair paternity and reproductive skew might lead to different conclusions. For example, the focal male may be selected to breed in philopatry with his father and stepmother even while achieving very low within-pair paternity due to his father's high relative heritable genetic quality.

Examining the inclusive fitness consequences for the interacting male of the focal male's dispersal decision reveals the zones in which conflict over settlement may occur. Because the inclusive fitness interests of the focal male and his father are aligned when the father is mated to the focal male's mother (Figures 3.7 and 3.9), the model predicts that a conflict over settlement will not arise between the males. However, a conflict over settlement may arise between the focal male and his stepfather when the focal male has the option of dispersing under low density, because the focal male's inclusive fitness is highest under the latter option while the stepfather's inclusive fitness is highest when the focal male is philopatric. (The stepfather gains higher inclusive fitness when interacting with the focal male than when breeding solitarily because the stepfather sires extra-pair offspring in the philopatric focal male's nest, while he sires no extra-pair offspring when breeding solitarily.) The focal male's inclusive fitness interests are not aligned with those of a related male (i.e., his father or brother) mated to an unrelated female over a large heritable genetic quality range, assuming that dispersal under low density is an option for the focal male (Figures 3.8 and 3.10). When dispersal under low density is not an option for the focal male, the zone of settlement conflict disappears, indicating that the potential for conflict depends importantly upon the available breeding opportunities. Evaluating the predicted

outcomes of these settlement conflicts is beyond the scope of the current model, but represents an interesting avenue for future research.

Empirical tests and extensions

The model has key implications for empirically testing the effects of relatedness on extra-pair mating behavior and extra-pair mating behavior on philopatry. Importantly, the model predicts that relatives will gain a higher proportion of paternity than nonrelatives only when the nonrelative in question has higher heritable genetic quality than the focal male. Thus, it is unsurprising that empirical studies have not revealed a higher than expected degree of relatedness among males and the extra-pair sires of their broods (Huyvaert and Parker 2010), as the predicted relationship may only hold for a subset of males. In species in which age can be used as a proxy for heritable genetic quality, the model predicts that older related males, but not same-age or younger related males, will gain a higher proportion of extra-pair paternity than nonrelatives. Other factors that might affect the opportunity to gain extra-pair copulations, such as the distance between territories, should be controlled for in such comparisons.

With respect to philopatry, the model predicts that natal dispersal distances will be shorter under high density than under low density. This prediction resembles that of the habitat saturation hypothesis, which predicts that individuals will be more likely to remain resident on the natal territory than disperse and breed under high density than under low density (Brown 1974); the key difference is that we consider individuals that have already made the decision to disperse and breed, but may do so at varying distances from the natal territory. Our prediction is supported in bicolored wrens, *Campylorhynchus griseus* (Austad and Rabenold 1986). Ecological factors are

perhaps less likely to complicate this comparison than are behavioral factors, as one might expect that individuals would be forced to disperse farther in order to find a vacant territory under high density than under low density, a pattern opposite to the model's prediction. However, behavioral factors such as assistance from relatives in establishing a territory could result in a pattern similar to that predicted because, under high density, such assistance might be both more important and more likely to take the form of space-sharing or territorial budding. Tests of this prediction could address this potential complication through investigating the process of territory establishment, or excluding overlapping territories from analysis.

Several modifications to increase the biological realism of the model are possible, only two of which we mention here. First, because real extra-pair mating interactions among breeding males are frequently but not exclusively dyadic (Chapter 1), structuring the model such that multiple males may compete for extra-pair paternity in the same brood could yield important results. Examining competition among three related males would be especially interesting, and one might predict that skew would similarly favor the male with highest relative heritable genetic quality. Second, we assumed that females do not invest in conflict over extra-pair paternity at the expense of parental investment, a simplifying assumption that is supported by previous work showing this is the case under a biologically realistic range of parameters (Chapter 1). However, female investment in this conflict may occur in some cases (Chapter 1), and examining the selection on conflict investments by related (i.e., mothers) versus unrelated females would be particularly valuable.

Conclusions

We used a game theoretic model to first examine whether genetic relatedness among breeding males contributes to maintaining extra-pair mating behavior. We found that males are selected to invest less energy in preventing extra-pair paternity loss to 1) relatives than nonrelatives, and 2) relatives having higher heritable genetic quality than relatives having lower heritable genetic quality. Considering investments in conflict by both players, the outcome is that relatives having higher genetic quality than the focal male gain a higher proportion of paternity than nonrelatives. Second, we examined whether competition with relatives over extra-pair paternity represents a cost or benefit of philopatry, finding that competition with relatives yields higher inclusive fitness benefits than competition with nonrelatives in this context: reduced investment in conflict among relatives decreases the costs of competition. This result indicates that the reduced costs of extra-pair paternity competition with relatives versus nonrelatives may contribute to the evolution of philopatry in genetically non-monogamous populations. Importantly, these inclusive fitness benefits arise even when measures such as extra-pair paternity and reproductive skew seem to indicate intense competition between relatives over paternity. Recent genetic analyses have revealed that kin structure in populations with no apparent cooperative behaviors is likely much more common than previously realized (Hatchwell 2010); we suggest that examining the potential contribution of inclusive fitness benefits derived from extra-pair mating behavior among male relatives may be a fruitful line of future research in explaining the evolution of this kin structure.

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APPENDIX 3.1

The inclusive fitness consequences of extra-pair paternity among relatives

Under which conditions do fathers gain inclusive fitness benefits from avoiding targeting sons' mates for extra-pair fertilizations, and do sons gain inclusive fitness benefits from losing paternity to fathers rather than unrelated males? We examine the inclusive fitness consequences of extra-pair mating interactions between fathers and sons, and ask when conflict over extra-pair paternity between father and son may arise.

Variables and inclusive fitness functions

r_a = father's relatedness to his within-pair young

r_x = father's relatedness to his extra-pair young

r_s = father's relatedness to his son's within-pair young

r_w = son's relatedness to within-pair young in his brood

r_e = son's relatedness to extra-pair young in his brood

r_f = son's relatedness to his father's extra-pair young

r_h = son's relatedness to his father's within-pair young

p_a = proportion of father's brood that father sires

p_x = proportion of extra-pair brood that father sires

p_w = proportion of son's brood that son sires

p_e = proportion of son's brood that extra-pair male sires

IF_f = father's inclusive fitness = $(p_a * r_a) + (p_x * r_x) + (p_w * r_s)$

IF_s = son's inclusive fitness = $(p_w * r_w) + (p_e * r_e) + (p_x * r_f) + (p_a * r_h)$

Key assumptions

1. The population is diplo-diploid and inbreeding does not occur ($r_a = r_x = 0.5$, $r_w = 0.5$).

2. The father is the son's genetic as well as social father ($r_s = 0.25$, $r_f = 0.25$).

3. The father is mated to the son's mother ($r_h = 0.5$).

4. The son does not gain extra-pair paternity (EPP).

5. The father does not lose within-pair paternity ($p_a = 1$).

6. When the father gains EPP, the proportion of EPP he gains is equal to the proportion of paternity that the son loses when he loses paternity to an extra-pair sire. Here, we assume that this fixed proportion is equal to one half.

Cases for comparison

Case	Father's inclusive fitness	Son's inclusive fitness
1. Father gains no extra-pair paternity; son loses no paternity	0.75	1
2. Father gains no extra-pair paternity; son loses paternity to a nonrelative	0.625	0.75
3. Father gains extra-pair paternity in a nonrelative's brood; son loses no paternity	1	1.125
4. Father gains extra-pair paternity in a nonrelative's brood; son loses paternity to a nonrelative	0.875	0.875
5. Father gains extra-pair paternity in the son's brood	0.875	0.875

Conclusions

1. The son always does best by maintaining complete within-pair paternity: his inclusive fitness is higher in cases 1 and 3 than in cases 2, 4, and 5.

2. The father always does best by gaining EPP: his inclusive fitness is higher in cases 3, 4, and 5 than in cases 1 and 2.

3. If the son will inevitably lose paternity, but his father can gain EPP in a nonrelative's nest, both son and father gain equal inclusive fitness whether the father targets the son (case 5) or a nonrelative (case 4) for paternity gain.

4. If the son will inevitably lose paternity, and his father can only gain EPP in the son's nest, both son and father gain higher inclusive fitness when the father gains EPP in the son's nest (case 5) than when the son loses paternity to a nonrelative (case 2).

5. If the father can only gain EPP in his son's nest, the father gains higher inclusive fitness from doing so (case 5) than from avoiding siring young in his son's nest (case 1). However, the son's inclusive fitness is higher when he maintains complete paternity and his father gains no EPP (case 1) than when he loses paternity to his father (case 5).

6. Overall, when paternity loss by the son is inevitable, and the father's options for acquiring EPP are limited, the genetic interests of the males align in favoring paternity loss to the father over paternity loss to a nonrelative. When paternity loss by the son is avoidable, conflict may arise between father and son over the father siring young in the son's brood.

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CHAPTER 4

CRYPTIC COOPERATION IN WESTERN BLUEBIRDS: KIN NEIGHBORHOODS SET THE STAGE FOR OPPORTUNISTIC MALE-MALE COALITIONS

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ABSTRACT

The association of individuals with their relatives in kin-structured populations may lead to the evolution of cooperation by kin selection, either when such associations occur through delayed dispersal and helping at the nest or through formation of "exploded" family groups, with family members resident on spatially clustered but independent breeding territories. Here we show that kin neighborhoods set the stage for opportunistic male-male defensive coalitions in the contexts of experimentally-simulated territorial intrusion and predator attack in western bluebirds. We found that on average over one-third of males have at least one first-order male relative breeding onsite, and all extraterritorial responders of known relatedness in both of our experiments were first-order male relatives of the focal males. However, living in an exploded family group does not confer levels of cooperative defense commensurate with those gained through intraterritorial group living: in both experiments, males with helpers were significantly more likely to receive responses from stay-at-home helpers than males with adult male relatives breeding onsite were to receive responses from extraterritorial males. In combination with providing males with previously demonstrated opportunities to return home to help, living in exploded family groups may also confer benefits in dire situations, such as during territorial intrusions and anti-predator defense. This study represents an initial step toward identifying cryptic cooperative behaviors

that are expressed in kin neighborhoods and which differ between stay-at-home and dispersed relatives.

INTRODUCTION

The association of individuals with their relatives in kin-structured populations is a taxonomically widespread phenomenon that may lead to the evolution of cooperation by kin selection (Hamilton 1964a; Hamilton 1964b; Stacey and Koenig 1990; Bourke and Franks 1995; Koenig and Dickinson 2004; Bourke 2011). Among vertebrates, associations of related individuals may occur either in "intraterritorial" family groups, with family members resident on a single territory (Stacey and Koenig 1990), or in "exploded" family groups (c.f. "classical" versus "exploded" leks; Gilliard 1963; Bradbury 1977), with family members resident on spatially clustered but independent territories (Dickinson and Hatchwell 2004). Exploded family groups are found in several territorial bird species including western bluebirds (*Sialia mexicana*; Dickinson, Koenig, and Pitelka 1996; Kraaijeveld and Dickinson 2001), long-tailed tits (*Aegithalos caudatus*; Hatchwell et al. 2001; Russell 2001), and Karoo scrub-robins (*Cercotrichas coryphaeus*; Ribeiro et al. 2012), all of which also exhibit cooperation in the form of helping to raise non-descendent young ("helping at the nest"; Skutch 1935), as well as colonial species such as white-fronted bee-eaters (*Merops bullockoides*; Emlen and Wrege 1988).

Exploded family groups may also occur in species with no known cooperative behaviors: kin structure occurs in many populations both of cooperative species and those in which cooperative behavior is as yet undescribed (Hatchwell 2010). The prevalence of kin structure in studied

populations suggests that exploded family groups may be a more important context for the evolution of social behavior than previously suspected (Hatchwell 2010). However, it is as yet unclear how living in exploded family groups differs from living in intraterritorial family groups with respect to the potential benefits and automatic costs of group living (Alexander 1974).

Comparing cooperative behaviors among individuals in exploded versus intraterritorial family groups is one approach to examining the relative benefits of each mode of association with relatives. Both the type and frequency of cooperative behavior may vary between exploded and intraterritorial groups; we suggest that a distinction between incidental cooperative behaviors displayed in rare or emergency contexts (e.g., helping a relative defend against a conspecific intruder; Sherman 1981) and continuous cooperative behaviors displayed more regularly (e.g., feeding a relative's offspring; Emlen and Wrege 1989) is useful in this context, as the demands of independent breeding may mean that incidental rather than continuous cooperation is more common among individuals in exploded groups. In western bluebirds, independently breeding males may simultaneously feed their own and a relative's young, and failed breeders may help rear relatives' young (Dickinson, Koenig, and Pitelka 1996; Dickinson and Akre 1998), indicating that individuals maintain family relationships as adults and establishing that cross-territorial cooperation occurs. Two possible contexts in which cryptic, incidental cooperation among western bluebirds may occur are territory defense against conspecific intruders and defense against predators.

Cooperative territory defense by group members occurs in many social species (Grimes 1980; Kinnaird and Grant 1982; Hunter 1985; Zack 1986; VanderWerf and Strahl 1990; Lacey and

Sherman 1991; Farabaugh, Brown, and Hughes 1992; Burt and Peterson 1993; Wingfield and Lewis 1993; McComb, Packer, and Pusey 1994; Sherman 1995; Perry 1998; Putland and Goldizen 1998; Kraaijeveld and Dickinson 2001; Radford 2003; Seddon and Tobias 2003; Kleiber et al. 2007), but examples of cooperative defense by relatives living on independent territories are more uncommon (Sherman 1981). Similarly, cooperative defense against predators, including behaviors such as mobbing and alarm-calling, is common among group-living species (Lindeque and Kapner 1993; Sherman 1995; Perry 1998; Maklakov 2002; Arnold, Goldizen, and Owens 2005; Griesser and Ekman 2005; Graw and Manser 2007) and has been documented in some studies of independently breeding kin (Sherman 1977) but not others (Lessells, Avery, and Krebs 1994). Here, we take an experimental approach to comparing the frequency of these opportunistic cooperative behaviors between individuals living in exploded versus intraterritorial groups, asking to what extent those living in exploded family groups capture these potential benefits of group living.

Our study system is the western bluebird, a socially but not genetically monogamous species in which 7% of pairs have helpers (Dickinson, Koenig, and Pitelka 1996; Dickinson and Akre 1998). Strong male philopatry allows for extended interactions among adult kin: western bluebirds form winter social groups that may include offspring of the year in addition to older male offspring that have bred independently (Kraaijeveld and Dickinson 2001). Winter social group members cooperatively defend winter territories (Kraaijeveld and Dickinson 2001; Kleiber et al. 2007), setting a precedent for cooperative defense among individuals with independent breeding experience. Additionally, cooperation between relatives across territory boundaries occurs during the breeding season: a small proportion of males behave as simultaneous breeder-

helpers, feeding their own nestlings while also feeding the nestlings of nearby relatives (Dickinson and Akre 1998). Thus, this species represents an interesting intermediate between those in which the majority of breeding units consist of intraterritorial family groups and those in which kin structure but not cooperative behavior is known to occur. The relative ease with which field experiments and accompanying behavioral observations can be conducted in this species is also important, because cooperative behaviors that occur opportunistically in response to rare predation attempts or threats to territory ownership may be difficult to observe even with intensive behavioral monitoring.

Here, we first establish the extent to which kin are clustered in the western bluebird population, focusing on breeding males that are putative first-order relatives. We then evaluate cooperative defense responses in experimental simulations of 1) territorial intrusion by a conspecific and 2) predator attack, assessing the effects of relative presence and interbox distance on the likelihood of receiving a response. Finally, we compare the effects of exploded versus intraterritorial group living on cooperative defensive behavior. If males breeding independently suffer a reduction in the availability of coalition partners for opportunistic cooperative defense, we predict that males with adult male relatives breeding onsite will receive significantly fewer responses from extraterritorial males than males with helpers will receive from helpers.

METHODS

Study population

Details of the long-term monitoring of the western bluebird population at Hastings Natural History Reservation, Carmel Valley, California, are described elsewhere (Dickinson, Koenig,

and Pitelka 1996). Briefly, nest boxes and any discovered natural cavity nests were monitored intensively throughout the breeding season. Eggs were labeled and weighed as they were laid. All nestling bluebirds were measured, blood sampled, and given unique color band combinations, as were all captured adult bluebirds. Associations of birds with nests were determined through intensive 90-min feeding behavior observations, which were conducted when nestlings were 4-6, 9-11, and 14-16 days old, as well as opportunistic observations during nest box censuses. Adult bluebirds were identified by color band re-sighting using binoculars and spotting scopes. Most breeding groups consist of socially monogamous pairs, although pairs with adult male helpers and juvenile helpers of either sex also occur (Dickinson, Koenig, and Pitelka 1996). We maintain a long-term database that includes all breeding attempts and social relationships, from which we can derive pedigree relatedness values.

Kin structure

We quantified both the number of dyads of first-order related (i.e., coefficient of relatedness, r=0.5) breeding adult males and the proportion of breeding adult males (hereafter "males) that have breeding adult male first-order relatives (hereafter "relatives") on the study site. Our data set included 294 unique breeding males over 12 years (2000-2011, inclusive).

For each year, we scored the number of unique father-son and full brother-full brother dyads occurring on the site. For example, if a father and three of his full brother sons all bred on the study site in a single year, we scored this as three father-son dyads and three full brother dyads. We also scored the proportion of males that were involved in at least one father-son or full brother-full brother dyad each year. For example, if a father and three of his sons all bred on the

study site in a single year, we scored this as four males involved in at least one dyad. We scored the relationships according to pedigree rather than genetic relatedness: full brothers are defined as males with the same social mother and father, while fathers are social fathers but necessarily genetic fathers due to the occurrence of extra-pair paternity in the western bluebird population (Dickinson and Akre 1998; Ferree and Dickinson 2011). Evidence that males with extra-pair versus within-pair fathers do not use this information in determining whether to help at the nest of their mother and social father (Dickinson and Akre 1998) suggests that bluebirds may assess associational rather than genetic relatedness, as do species with similar social systems (Komdeur, Richardson, and Burke 2004; Sharp et al. 2005).

For the analyses of kin clustering, we used the 128 males having at least one first-order male relative breeding onsite and with an interbox distance of less than 1000 m in the years 2000-2011. We limited our analysis to interbox distances less than 1000 m in order to avoid extreme outliers. Some males occurred in multiple years such that the total number of male-year combinations was 176.

We investigated the extent to which relatives' territories are clustered together by taking the mean of all the interbox distances between a focal male and his nonrelatives, and comparing this to the mean of all the interbox distances between the same focal male and his relatives. When a focal male's relatives bred in more than one box in a given year, we used all the interbox distances in calculating that male's mean interbox distance with relatives. For example, if a male bred in Box 1 and had one brother who bred in boxes 2 and 3, and one brother who bred in boxes 4 and 5, we took the mean of the following interbox distances: 1 to 2, 1 to 3, 1 to 4, and 1 to 5.

When a focal male bred in more than one box in a given year, we again used all the interbox distances in calculating the male's mean interbox distance with relatives. For example, if a male bred in boxes 1 and 2, and his father bred in boxes 3 and 4, we took the mean of the following interbox distances: 1 to 3, 1 to 4, 2 to 3, 2 to 4. When a male bred multiple times in the same box, we did not alter our calculation of interbox distance means, i.e., each interbox distance was only included once in each mean calculation. If relatives' territories are clustered, the mean interbox distance between relatives will be significantly smaller than the mean interbox distance between nonrelatives.

We investigated the tightness of kin-biased clustering by calculating the interbox distances to each male's nearest kin neighbor and nearest nonkin neighbor. If relatives are tightly clustered, the interbox distance between males and their nearest kin neighbors will be significantly smaller than the interbox distance between males and their nearest nonkin neighbors.

Territorial intrusion experiment

The territorial intrusion experiment tested whether males form facultative coalitions in the face of a threat to territory ownership. We conducted this experiment at focal nests when the nestlings were at least nine days old. Two observers (C.A.S. and a field assistant) were present during each experiment. For each experiment, we captured an adult male off the study site (5 to 30 miles from the study site boundary) for use as an unfamiliar decoy. Before and after the experiment, the decoy was kept in a large cage and provided with water and live meal worms *ad libitum*. To avoid pseudoreplication, we used 19 different decoy males over the 72 trials we conducted. We carried the decoy to the focal territory in a small cage covered with a towel and placed the cage 5

m from the focal nest box. One observer removed the towel from the cage, then moved to join the second observer at a distance of 30-40 m from the cage. The observation period did not begin until at least one of the focal pair members was within 20 m of the cage. One observer was responsible for recording the band combination and behavior of the focal male, while the second observer was responsible for recording the band combination and behavior of the focal female as well as any responders. The observers read bluebirds' color bands using binoculars and spotting scopes, recorded observations using voice recorders, estimated distances visually, and recorded the time to the second for each observation. The observation period lasted 20 min, after which one observer placed the towel over the cage and removed the decoy from the territory. All decoys were released at their capture location. A response was scored only if the responding bluebird entered within a 20 m radius of the cage containing the decoy and displayed defensive behaviors such as alarm-calling or swooping over the cage. The responder's identity was scored only if all four bands were sighted and recorded.

Distress vocalization experiment

The distress vocalization experiment tested whether males receive assistance responses during attack by a predator. We simulated predator attack using playbacks of the distress calls that western bluebirds, similar to many other bird species (Norris and Stamm 1965; Rohwer, Fretwell, and Tuckfield 1976; Perrone Jr 1980; Inglis et al. 1981; Hogstedt 1983; Koenig et al. 1991), emit when captured. We recorded male distress vocalizations from captured males during the egg-laying period; we attempted to incite distress vocalizations by holding the captured male upside down. Because many males did not produce distress calls, we also recorded calls from unfamiliar males (males captured 5-30 mi from the primary study site bounday) to play back

when we did not have the focal male's own distress call. Call clips ranged from 5-10 s; recorded calls longer than 10 s were edited for length using the program GoldWave (GoldWave, Inc.). We used each unfamiliar male's distress call in no more than 5 trials to avoid pseudoreplication. Overall, in 76% (44/58) of trials we used an unfamiliar male's distress call, in 21% (12/58) of trials we used the focal male's pre-recorded distress call, and in 3% (2/58) of trials the male produced a natural scream during the experiment. We made all recordings using a Sennheiser ME66 shotgun microphone and an M-Audio MicroTrack II digital audio recorder, and we played calls using an Apple iPod Nano and Logitech Pure-Fi omnidirectional speakers.

We conducted the experiment at focal nests when the nestlings were at least nine days old. Two observers (C.A.S. and a field assistant) were present during each experiment. We captured the breeding male using a box trap. One observer stood 5 m from the nest box and held the breeding male aloft in her hand. The experiment began when the observer holding the male started the playback. The experiment duration was 10 min from the beginning of playback. All calls were played twice: once to begin the experiment and again 1 min after the beginning of the experiment. The second observer recorded the identities and behaviors of any bluebirds that moved within 20 m of the captive male, including the breeding female, the helper(s) if applicable, and any extraterritorial birds. At the conclusion of the experiment, we released the focal male on his territory. A response was scored only if the responding bluebird entered within a 20 m radius of the captive male and displayed defensive behaviors such as alarm-calling or swooping over the captive male. The responder's identity was scored only if all four bands were sighted and recorded.

Statistical Analyses

1. *Kin structure*

We used a Spearman's rank correlation to test whether the proportion of males having relatives in a given year was affected by the total number of breeding males. We used a Wilcoxon signed rank test to determine whether one dyad type (father-son or brother-brother) was more common than the other across years.

To determine the degree of kin clustering, we tested the effect of neighbor type (relative or nonrelative) on mean interbox distance using a Generalized Linear Mixed Model (GLMM) with male ID, year, and number of relatives as random effects. To test whether an effect could be the result of males with relatives living in neighborhoods in which all territories are more tightly clustered (due to, e.g., a higher density of important resources), we used a Spearman partial rank-order correlation to test for an association between a focal male's mean interbox distances to relatives and nonrelatives, while controlling for male ID. We used Spearman partial rank-order correlations controlling for male ID to test the effect of a male's number of relatives on 1) the ratio of mean interbox distance with relatives to mean interbox distance with nonrelatives, and 2) the mean interbox distance with relatives.

To determine the tightness of kin clustering, we tested the effect of neighbor type (relative or nonrelative) on distance to the nearest neighbor using a GLMM with male ID, year, and number of relatives as random effects. We used Spearman partial rank-order correlations controlling for male ID to test the effect of the number of relatives a male had on 1) the ratio of distance to the

nearest related neighbor to distance to the nearest unrelated neighbor, and 2) distance to the nearest related neighbor.

2. *Territorial intrusion and distress vocalization experiments*

For each experiment, we first tested the hypothesis that having at least one first-order male relative breeding onsite influences the likelihood that a male will receive a response during the experiment using a Fisher's exact test. We then tested whether the number of first-order male relatives a focal male had onsite affected his likelihood of receiving a response using a GLMM with the binomial error distribution and a logit link, including male ID and year as random effects, first among only males having first-order male relatives onsite and second among all males. Next, we examined whether proximity affects the likelihood of response by using a GLMM with the binomial error distribution and a logit link to test the effect of interbox distance to the nearest relative on likelihood of receiving a response, including male ID, year, and number of relatives as random effects. For the territorial intrusion experiment, we next tested whether males whose nearest neighbor is a first-order male relative are more likely to receive a response than males who have relatives onsite but whose nearest neighbor is not a first-order relative using a Fisher's exact test. We also tested whether the mean ranks of nearest relative distance differed between males receiving or not receiving a response using a Wilcoxon rank sum test. Finally, for both experiments, we tested whether males with helpers were significantly more likely to receive responses from helpers than were males with adult male relatives breeding onsite to receive responses from extraterritorial males using a Fisher's exact test.

We present all means as ± standard error unless stated otherwise. All tests were two-tailed. We ran all statistical analyses in R 2.13.2, using the lme4 package for GLMMs (R Development Core Team 2011).

Ethical note

The protocols for capturing, handling, and observing western bluebirds were approved by the Cornell University Institutional Animal Care and Use Committee Protocol (no. 2005-0137) and conducted under permits from the United States Geological Survey Bird Banding Lab (no. 23533), the California Department of Fish and Game (no. 9372), and the United States Fish and Wildlife Service (no. MB20494A-0).

RESULTS

1. Kin structure

Over one-third of males have first-order male relatives breeding onsite

As predicted from previously known patterns of male philopatry (Kraaijeveld and Dickinson 2001), we found extensive kin structure in the western bluebird population. Over the 12 years (2000-2011) we examined, the mean number of breeding adult males (hereafter, males) having breeding first-order adult male relatives (hereafter, relatives) onsite was 15.83±2.31 (range 5 to 33) (Figure 4.1). The mean proportion of males having relatives onsite was 0.36±0.04 (range 0.20 to 0.61). The proportion of males having relatives in a given year was unaffected by the total number of breeding males (Spearman's rank correlation: $p>0.05$).

Among males having at least one relative onsite, the mean number of relatives per male was 1.5±0.05 (range 1-4). Sixty-five percent (123/190) of males had one relative onsite, 24% (46/190) had two relatives, 10% had three relatives (19/190), and 1% (2/190) had 4 relatives.

The mean number of first-order male relative dyads in the study population each year was 11.67±1.80 (range 3 to 22) (Figure 4.2). The majority of dyads were father-son dyads (66%±3%), and father-son dyads were significantly more common than full brother dyads (Wilcoxon signed-rank test: $p<0.005$).

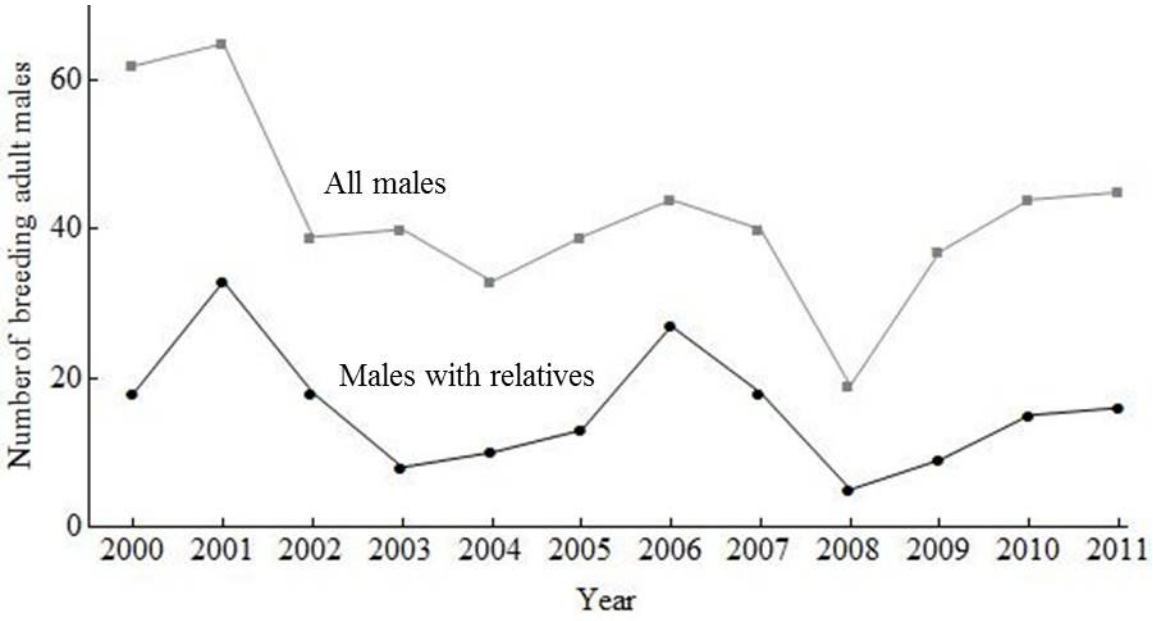

Figure 4.1 The number of males with at least one first-order male relative breeding onsite (black line) compared to the total number of breeding males (grey line) in the western bluebird population over the years 2000-2011. The mean number of breeding adult males having breeding first-order adult male relatives onsite was 15.83±2.31 (range 5 to 33). The mean proportion of breeding adult males having breeding adult male relatives onsite was 0.36±0.04 (range 0.20 to

0.61). The proportion of males having relatives in a given year was unaffected by the total number of breeding males (Spearman's rank correlation: $p>0.05$).

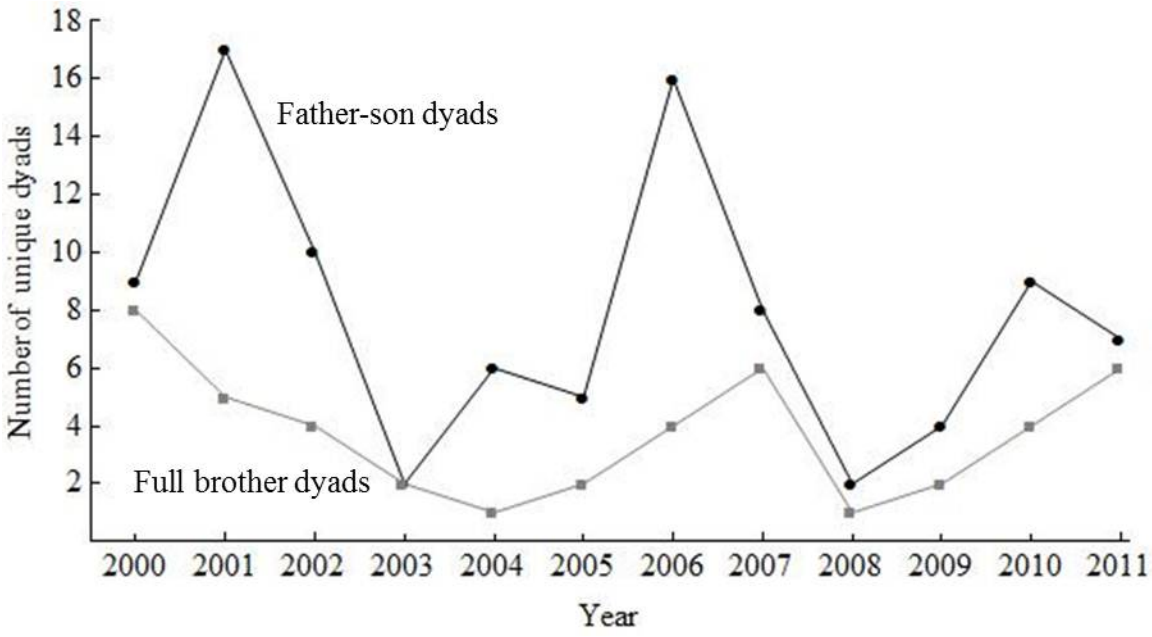

Figure 4.2 The number of unique father-son dyads (black line) compared the number of unique full brother-full brother dyads (grey line) in the western bluebird population over the years 2000-2011. The mean number of first-order male relative dyads in the study population each year was 11.67±1.80 (range 3 to 22). The majority of dyads were father-son dyads (0.66±0.033), and father-son dyads were significantly more common than full brother dyads (Wilcoxon signed-rank test: $p<0.005$).

Relatives are clustered, but having more relatives does not increase clustering

Among males with relatives onsite, the mean interbox distance to relatives was 313.6±14.3 m versus 607.52 m to nonrelatives. Neighbor type significantly affected mean interbox distance (GLMM: $F=444.2$, $p<0.0001$) such that the mean interbox distance to relatives was significantly

lower than the mean interbox distance to nonrelatives. No significant association existed between a focal male's mean distances to relatives and nonrelatives (Spearman partial rank-order correlation: $p>0.05$).

The ratio of mean interbox distance with relatives to mean interbox distance with nonrelatives increased as the number of relatives increased (Spearman partial rank-order correlation: $R=0.23$, $p=0.002$), such that relatives were on average farther relative to nonrelatives for males with more relatives than for males with fewer relatives. Excluding the two observations of males with four relatives did not change this pattern (Spearman partial rank-order correlation: $R=0.22$, $p=0.003$). The mean interbox distance with relatives increased as the number of relatives increased (Spearman partial rank-order correlation: $R=0.25$, $p=0.0006$), such that relatives were on average farther for males with more relatives than for males with fewer relatives. Again, excluding the two observations of males with four relatives did not change this pattern (Spearman partial rank-order correlation: $R=0.24$, $p=0.001$).

Nearest neighbors are more likely to be nonrelatives than relatives

For 33.0% (58/176) of males with relatives breeding onsite, the nearest neighbor was a relative. Reflecting the fact that the minority of males with relatives have a related nearest neighbor, the mean distance to the nearest related neighbor was 265.9±14.2 m versus 158±5.5 m to the nearest unrelated neighbor. Neighbor type (relative or nonrelative) significantly affected the distance to the nearest neighbor (GLMM: $F=54.4$, $p<0.0001$), such that nearest unrelated neighbors were significantly closer than nearest related neighbors. This result indicates that the clustering of related males' territories is loose, with most males having unrelated nearest neighbors.

The ratio of distance to the nearest related neighbor to distance to the nearest unrelated neighbor decreased with the number of relatives (Spearman partial rank-order correlation: R=-0.18, p=0.02), such that the nearest related neighbor was closer relative to the nearest unrelated neighbor for males with more relatives than for males with fewer relatives. Excluding the two observations of males with four relatives did not change this pattern (Spearman partial rank-order correlation: R=-0.17, p=0.03). However, the number of relatives had no effect on the distance to the nearest related neighbor either when the two males with four relatives were included (Spearman partial rank-order correlation: R=-0.14, p=0.06) or excluded (Spearman partial rank-order correlation: R=-0.12, p=0.12).

2. Territorial intrusion experiment

Responders were first-order male relatives

We conducted 72 trials over 2009-2011. An adult male that was not resident on the territory responded in 9 trials. However, we were only able to positively identify the responder in 5 trials due to incomplete color band reads for the responders in the other 4 trials. The 4 trials with unidentified responders were excluded from further analysis. We additionally excluded 3 trials due to incomplete information about the status of the focal male's relatives.

All 5 identified responders were first-order male relatives of the focal male. Responders were the father (1), son (2), or brother (2) of the focal male. Both of the brother responders and one of the son responders were breeders on independent territories. The other son responder was a helper on a different territory (his grandfather's). Although the father responder's status was unknown, his son's territory extended across the boundary of the study site and he may have been breeding

close by but off the site. We therefore coded the focal male whose father responded as having a male relative breeding onsite; excluding this trial does not affect the significance of the tests presented below. However, because we did not have an interbox distance between this responder and the focal male, we excluded the trial from our analyses of the effects of interbox distance on response.

Presence but not number of relatives affects response

The mean number of relatives per focal male was 0.71±0.12 (range=0-4). Focal males that had at least one first-order male relative onsite were significantly more likely to receive a response than males that had no first-order male relatives on site (Fisher's exact test: $p=0.01$, n=64 trials) (Table 4.1). However, the total number of relatives did not affect the likelihood of receiving a response during the experiment either among only males having first-order male relatives onsite (GLMM: $p>0.05$, n=27 trials) or among all males (GLMM: $p>0.05$, n=64 trials).

Table 4.1 The effect of having at least one first-order male relative onsite on a male's likelihood of receiving a response in the territorial intrusion experiment.

	Response	No response
Male has ≥1 first-order male relative breeding onsite	5	22
Male has no first-order male relatives breeding onsite	0	37

Distance does not affect response

Among males that had at least one first-order male relative onsite, those males whose nearest neighbor was a first-order male relative were not significantly more likely to receive a response than those males whose nearest neighbor was a nonrelative (Fisher's exact test: $p=0.6$, $n=26$ trials) (Table 4.2). Interbox distance with the nearest first-order male relative did not affect the likelihood of receiving a response (GLMM: $p>0.05$). Additionally, the mean ranks of nearest relative distance did not differ significantly between males receiving a response and males not receiving a response (Wilcoxon rank sum test: $p=0.07$) (Figure 4.3).

Table 4.2 The effect of having a related nearest neighbor on the likelihood of receiving a response in the territorial intrusion experiment for the 26 trials in which the focal male had a first-order male relative onsite with known interbox distance.

	Response	No response
Male's nearest neighbor is a first-order male relative	2	8
Male's nearest neighbor is a nonrelative	2	14

Figure 4.3 The distribution of interbox distances to the nearest relative among males that received a response (black bars) or did not receive a response (grey bars) during the territorial intrusion experiment. The males shown are the 26 that had adult male relatives breeding onsite. The mean ranks of nearest relative distance did not differ significantly between males receiving a response and males not receiving a response (Wilcoxon rank sum test: p=0.07).

Helpers respond more frequently than extraterritorial males

Of the 9 trials in which the focal male had an adult male helper at the nest, the helper met our criteria for response in 5 trials. Two of the males who received responses from males breeding on other territories had helpers, but no males received responses from both extraterritorial males and helpers. Males with helpers were significantly more likely to receive responses from helpers (56%; 5/9) than were male with adult male relatives breeding onsite to receive responses from extraterritorial males (23%; 5/22) (Fisher's exact test: p=0.04) (Table 4.3; Figure 4.4).

Table 4.3 Males with helpers were significantly more likely to receive responses from helpers than were male with adult male relatives breeding onsite to receive responses from extraterritorial males (p=0.04, Fisher's exact test).

	Response	No response
Male has a helper at the nest	5	4
Male has ≥1 first-order male relative breeding onsite	5	22

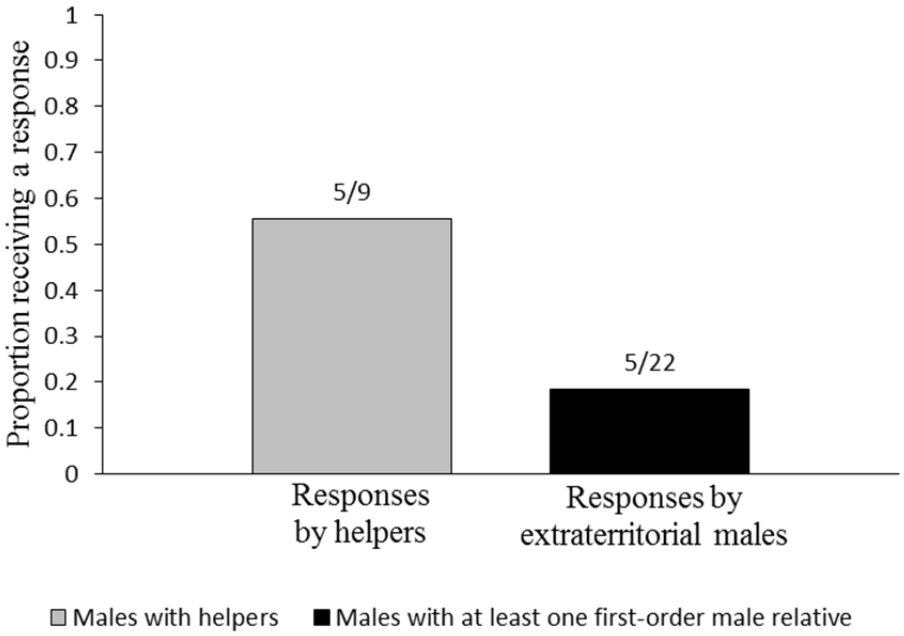

Figure 4.4 In the territorial intrusion experiment, males with helpers were significantly more likely to receive responses from helpers (56%; 5/9) than were male with adult male relatives breeding onsite to receive responses from extraterritorial males (23%; 5/22) (Fisher's exact test: p=0.04).

3. Distress vocalization experiment

Responders with known relatedness were first-order male relatives

We conducted 58 trials over 2009-2011. Individuals that were not resident on the territory responded in three trials. Responders were the focal male's son (1), the focal male's father (1), and an adult male accompanied by his juvenile son (1), both of unknown relatedness to the focal male. Relatedness was unknown in the latter case because the responding adult male was banded as an adult, and thus we had no information about his parentage. The focal male that received a response from two males of unknown relatedness had no known relatives onsite; he was breeding on the boundary of the study area and had been observed in the previous year but had no breeding attempt recorded onsite. Thus, we have insufficient information to determine whether the focal male and the responder were relatives.

Presence of relatives does not affect response

Males having at least one adult male relative breeding onsite were no more likely to receive responses than males with no relatives breeding onsite (Fisher's exact test: $p>0.05$, n=58 trials) (Table 4.4). The number of adult male relatives breeding onsite did not affect a male's likelihood of receiving a response either among only males with at least one relative (GLMM: $p>0.05$, n=23 trials), or among all males (GLMM: $p>0.05$, n=58 trials).

Distance does not affect response

Among males that had at least one first-order male relative onsite, interbox distance with the nearest first-order male relative did not affect the likelihood of receiving a response (GLMM: $p>0.05$, n=23 trials).

Table 4.4 Males having at least one adult male relative breeding onsite were no more likely to receive a response in the distress vocalization experiment than males with no known relatives breeding onsite ($p>0.05$, Fisher's exact test).

	Response	No response
Male has ≥1 first-order male relative breeding onsite	2	21
Male has no known first-order male relatives breeding onsite	1	34

Helpers respond more frequently than extraterritorial males

In 7 trials, the focal male had a single adult male helper, while in 1 trial, the focal male had two juvenile helpers. We excluded the trial with juvenile helpers from further analysis. The helper met our criteria for response in 4/7 trials. No males received responses from both extraterritorial males and helpers, and none of the males who received responses from males breeding on other territories had helpers. Males with helpers were significantly more likely to receive responses from helpers (57%; 4/7) than were male with adult male relatives breeding onsite to receive responses from extraterritorial males (10%; 2/21) (Fisher's exact test: $p=0.02$) (Table 4.5; Figure 4.5).

Table 4.5. Males with helpers were significantly more likely to receive responses from helpers than were male with adult male relatives breeding onsite to receive responses from extraterritorial males (p=0.02, Fisher's exact test).

	Response	No response
Male has a helper at the nest	4	3
Male has ≥1 first-order male relative breeding onsite	2	21

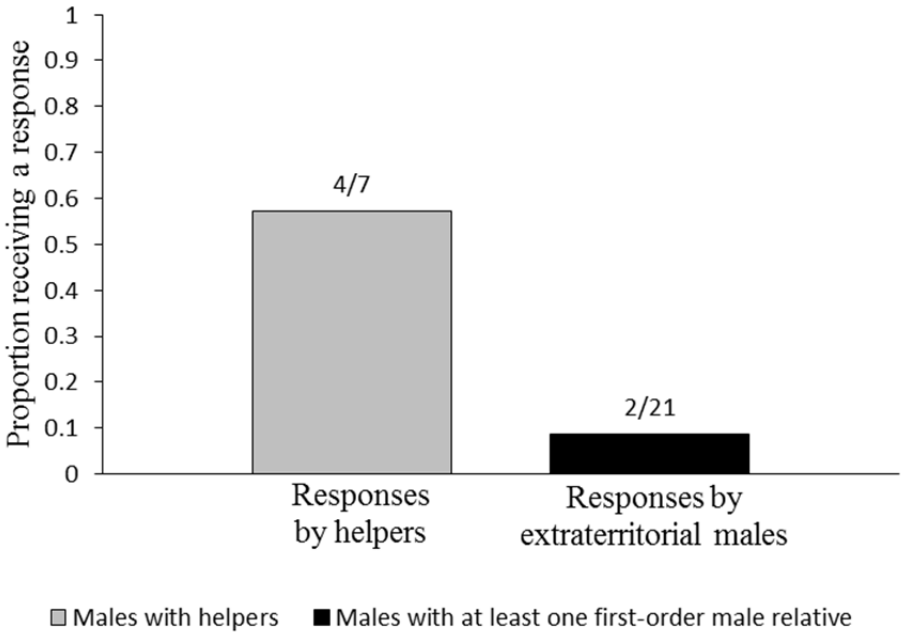

Figure 4.5 In the distress vocalization experiment, males with helpers were significantly more likely to receive responses from helpers (57%; 4/7) than were male with adult male relatives breeding onsite to receive responses from extraterritorial males (10%; 2/21) (Fisher's exact test: p=0.02).

DISCUSSION

Kin structure sets the stage for opportunistic male-male defensive coalitions in western bluebirds: we found that on average over one-third of males have at least one first-order male relative breeding onsite, and all extraterritorial responders of known relatedness in both of our experiments were first-order male relatives of the focal males. However, living in an exploded family group does not confer cooperative defense benefits commensurate with those gained through intraterritorial group living: in both experiments, males with helpers were significantly more likely to receive responses from helpers than were males with adult male relatives breeding onsite to receive responses from extraterritorial males. We discuss these results and their implications in further detail below.

First-order male relatives breed on clustered territories

Our analyses revealed extensive kin structure in the western bluebird population: on average 36±4% of males had at least one first-order male relative breeding onsite, more commonly a father or son than a full brother. The mean interbox distance to relatives was significantly lower than the mean interbox distance to nonrelatives, indicating that the territories of related males were spatially clustered. However, having more relatives did not increase the degree of clustering, as indicated by the mean interbox distance to relatives or the ratio of mean interbox distance to relatives to mean interbox distance to nonrelatives. Among males with relatives, the nearest neighbor was more likely to be a nonrelative than a relative: for only 33.0% (58/176) of males with relatives breeding onsite, the nearest neighbor was a relative. This result indicates that the clustering of related males' territories is loose, and suggests that clustered territories may arise through a settlement mechanism other than or in addition to territory budding (Woolfenden

and Fitzpatrick 1978), although this point requires further study. Overall, these results suggest high potential for opportunistic, kin-selected cooperative behaviors among western bluebird males, in addition to the continuous cooperative behaviors already known to occur (Dickinson, Koenig, and Pitelka 1996).

Extraterritorial coalition partners are first-order male relatives

In both of our experiments, all responders of known relatedness were first-order male relatives of the focal males. All responders were adult males, with the exception of a juvenile male that accompanied his responding father. These results indicate the importance of interactions among males in a population characterized by male philopatry and kin structure. Interestingly, although breeding males have mothers and, more rarely, sisters or daughters, onsite, no extraterritorial females responded during our experiments. This result is unsurprising for the territorial intrusion experiment, as the decoys we presented were male and previous work has shown that western bluebirds display higher intrasexual than intersexual aggression (Kleiber et al. 2007; Dickinson et al. 2009), but no previous work suggests an explanation for the lack of female relative response during the distress vocalization experiment.

In the territorial intrusion experiment, focal males that had at least one first-order male relative onsite were significantly more likely to receive a response than males that had no first-order male relatives on site. However, the number of relatives onsite, distance to the nearest relative, and whether the nearest neighbor was a relative did not affect a male's likelihood of receiving a response. In the distress vocalization experiment, the presence of relatives, the number of

relatives, and distance to the nearest relative did not affect a male's likelihood of receiving a response.

Intraterritorial family group members are more likely to respond than exploded family group members

Although all responders of known relatedness in both experiments were first-order male relatives, responses were rare: of males with at least one relative onsite, only 23% (5/22) received responses in the territorial intrusion experiment, and 10% (2/21) in the distress vocalization experiment. In contrast, males having adult male helpers received responses from those helpers with significantly higher frequency: 56% (5/9) and 57% (4/7) of males with helpers received responses from helpers in the territorial intrusion experiment and the distress vocalization experiment, respectively. These findings indicate that, although adult male relatives breeding independently may represent potential coalition partners in rare emergencies, helpers without their own breeding territories may be more reliable partners in cooperative defense. Males breeding in exploded family groups may thus enjoy increased cooperative defense benefits over males lacking relatives, but living in exploded groups does not confer cooperative defense benefits commensurate with those gained through intraterritorial group living.

Conclusions

Male western bluebirds in the focal population breed in the context of significant kin structure. Our results suggest that this kin structure facilitates the formation of cooperative defense coalitions, a form of opportunistic cooperation. However, we also found that males living in exploded groups gain reduced cooperative defense benefits compared to males living in

intraterritorial groups. An interesting direction for future research is whether individuals in exploded groups suffer reduced costs, e.g. forgoing reproduction when serving as a helper, compared to individuals living in intraterritorial groups. Living in exploded family groups may confer a different set of benefits and costs to those gained by living in intraterritorial family groups; this study represents an initial step in comparing the cooperative behaviors concomitant with these two modes of association with relatives. Additionally, our results suggest that even in a population in which many cooperative behaviors are well-characterized, opportunistic cooperation may occur in rare contexts. We suggest that cryptic cooperative behaviors (Hatchwell 2010) may best be studied using similar experiments in species in which kin structure exists but no cooperative behaviors have been documented.

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CHAPTER 5

EXTRA-PAIR PATERNITY AND MATING INTERACTIONS AMONG RELATED MALES IN WESTERN BLUEBIRD KIN NEIGHBORHOODS

Caitlin A. Stern and Janis L. Dickinson

ABSTRACT

Although kin structure, or the spatial clustering of relatives, may affect selection on both cooperative and competitive behaviors among kin, few empirical studies have investigated the effects of relatedness on extra-pair mating and extra-pair paternity. Here, we used a kin-structured western bluebird population to investigate first whether different male family members (e.g., fathers, brothers, sons) differ in their investments in seeking paternity in relatives' broods. Through observations of extra-pair mating behavior facilitated by temporarily detaining breeding males, we found that fathers were significantly more likely to intrude onto the detained male's territory than brothers or sons, but not more likely than stepfathers. Using genetic data, we found that 21% of identified extra-pair sires were first-order male relatives of the social father, but sons were not more likely to lose paternity to fathers than equidistant stepfathers. Second, we asked whether breeding near the son of one's mate provides a paternity buffer. We found that fathers with neighboring sons retained a significantly higher proportion of within-pair paternity than stepfathers with neighboring stepsons, providing support for the son assistance hypothesis for paternity buffering. While the genetic mating system has recently been shown to affect selection on kin structure, our results suggest that kin structure may also affect selection on the genetic mating system.

INTRODUCTION

Kin structure, where relatives are spatially clustered due to philopatry (Hatchwell et al. 2001; Russell 2001) or joint dispersal (Koenig et al. 2000; Ridley 2011), has been documented in an increasingly large number of species, including those with and without described cooperative behaviors (Hatchwell 2010). Although the presence of nearby kin facilitates kin-directed cooperative behavior (Kraaijeveld and Dickinson 2001; Russell and Hatchwell 2001), kin structure also permits potentially costly competition among relatives (Hamilton and May 1977). Within the majority of socially monogamous bird species, females are genetically polyandrous and produce offspring that are sired by extra-pair males. As a consequence, paired males face the possibility of expending time and energy caring for unrelated nestlings, while also suffering a reduction in direct fitness (Webster et al. 1995). Empirical investigations of potential biases in extra-pair paternity due to relatedness are as yet few (Huyvaert and Parker 2010). Interactions among kin and nonkin over extra-pair parentage thus represent an interesting and relatively unexplored example of competition and cooperation among relatives.

Western bluebirds (*Sialia mexicana*) are socially monogamous passerines in which extra-pair mating behavior is common: 19-22% of offspring in 45% of broods are sired by extra-pair fathers (Dickinson and Akre 1998; Ferree and Dickinson 2011). Western bluebirds resident on our long-term study site in central-coastal California exhibit male philopatry, which leads to extensive kin structure in the population: on average, 36% of breeding males have first-order male relatives breeding onsite each year (Chapter 4). Previous observations of redirected helping behavior, simultaneous breeder-helpers, and responses by extra-territorial males in the context of territory defense (Dickinson, Koenig, and Pitelka 1996; Dickinson and Akre 1998; Stern and

Dickinson, Chapter 4) indicate the importance of cross-territorial interactions among male family members in this population, as do previous records of intrusions by related males during male detention experiments (Dickinson 2001). Here, we use the western bluebird system to examine two primary questions concerning extra-pair mating interactions among male family members in kin neighborhoods.

First, regarding competition over paternity in kin neighborhoods, we ask whether male family members differ in their investments in gaining paternity in a focal male's nest. Given the inclusive fitness benefits of losing paternity to relatives versus nonrelatives, males may be selected to invest less effort in guarding against relatives' extra-pair copulation attempts than against nonrelatives' extra-pair copulation (EPC) attempts (Huyvaert and Parker 2010). However, this prediction addresses only the guarding male's behavior, and makes no reference to the conditions under which an EPC-seeking male is selected to target or avoid related males' mates. Conflict between relatives over extra-pair paternity is the subject of a game theoretic tug-of-war model, the results of which are discussed elsewhere (Chapter 3). Using this model, we show how known mean relatedness values among specific types of relatives (e.g., social father and son) can be used to derive population-specific predictions for how much individuals should invest in seeking extra-pair copulations with relatives' mates. We cannot directly test the predictions of the model in the western bluebird population because the predictions hinge upon the relative heritable genetic qualities of the interacting males. Heritable genetic quality may be correlated with age due to viability selection (Kokko and Lindstrom 1996; Kokko 1998), and western bluebird females prefer older extra-pair mates (Ferree and Dickinson 2011). However, we have not direct measured heritable genetic quality in western bluebirds. Here, we examine

male family members' behavioral investments in extra-pair mating, revealed by a male detention experiment that temporarily prevents mate guarding by the detained male. We combine these behavioral results with actual paternity outcomes revealed through genotype analysis, and discuss the resulting patterns in the context of the model's predictions.

Second, regarding cooperation over paternity in kin neighborhoods, we ask whether breeding near the son of one's mate provides a "paternity buffer"(Greene et al. 2000). This idea was first put forth for unrelated aggregations of lazuli buntings (*Passerina amoena*), in which brightly-colored males allow dull-colored males to settle on adjacent territories, thereby gaining a buffer against paternity loss to preferred brightly-colored males (Greene et al. 2000). We identify two possible mechanisms by which such a "paternity buffer" could function in kin-structured populations. First, because western bluebirds generally avoid incest (Dickinson and Akre 1998), a male whose neighbor is his mate's son experiences no threat to his paternity from his son or stepson, and this could reduce his paternity loss through a dilution effect ("incest avoidance hypothesis"). Second, because sons receive greater inclusive fitness benefits from the production of full siblings over half-siblings, sons may be selected to assist their fathers in mate guarding, for example, by chasing away intruding males that attempt to copulate with their mothers, a behavior previously observed in western bluebirds (Dickinson 2001) ("son assistance hypothesis"). We can distinguish between these two hypotheses by comparing the paternity losses of fathers versus stepfathers breeding near the female's sons: if incest avoidance results in decreased paternity loss, fathers and stepfathers will experience equivalent rates of paternity loss in the presence of a neighboring son, all else being equal. However, if sons assist with mate guarding, fathers, but not stepfathers, will experience reduced paternity loss when their mate's

son is nearby. In other words, because the son is presumably equally related to the stepfather and any of his mother's potential extra-pair mates, he receives no inclusive fitness benefit from assisting his stepfather in mate guarding. This question is not completely addressed by the aforementioned tug-of-war model (Chapter 3) because the model considers only dyadic interactions between males breeding separately, without considering the influence of a third interacting male. As a consequence, the earlier model assumes that a male interacting with the son of his mate will suffer no paternity loss. The son assistance hypothesis for paternity buffering in kin-structured populations invokes a triadic interaction: by breeding near one male, a second male gains protection from extra-pair paternity loss to a third male. We investigate this question using both behavioral evidence from field male detention experiments and genetic paternity analysis.

METHODS

The model

The details of the model formulation and analysis are described elsewhere (Stern, Dickinson, & Reeve; Chapter 3) but, briefly, we used a game theoretic, tug-of-war modeling approach (Reeve, Emlen, and Keller 1998) to examine the relationship between genetic relatedness among breeding males and extra-pair mating behavior in kin-structured populations. The variables included in the model are displayed in Table 1. In the previous analysis, we used coefficient of genetic relatedness values for interacting relatives that did not take into account the possibility of prior extra-pair paternity (e.g., we used the father-son relatedness value 0.5). This approach is appropriate when individuals use kin recognition mechanisms such as self-referent phenotype matching (Mateo and Johnston 2000; Neff and Sherman 2005). However, when individuals use

e.g. associational cues such as presence at the nest to recognize kin (Sharp et al. 2005), which is likely the case in western bluebirds (Dickinson and Akre 1998; Dickinson 2004), behavioral decisions may instead be based upon mean relatedness values. Thus, to make predictions specific to the western bluebird system, we used previously calculated mean relatedness values among the relevant relative types (Dickinson and Akre 1998) (Table 2). As detailed elsewhere (Stern, Dickinson, & Reeve; Chapter 3), we solved the model numerically to generate predicted values of optimal investments in seeking extra-pair copulations.

Table 1. Definitions of variables included in the tug-of-war model of Stern, Dickinson, and Reeve (Chapter 3).

Variable	**Definition**	**Possible values**
x_1	Male 1's investment in gaining extra-pair paternity (EPP) in Male 2's brood (Brood 2)	$0 \leq x_1 \leq 1$; $x_1 + y_1 \leq 1$
y_1	Male 1's investment in thwarting Male 2's attempts to gain EPP in Male 1's brood (Brood 1)	$0 \leq y_1 \leq 1$; $x_1 + y_1 \leq 1$
x_2	Male 2's investment in gaining EPP in Brood 1	$0 \leq x_2 \leq 1$; $x_2 + y_2 \leq 1$
y_2	Male 2's investment in thwarting Male 1's attempts to gain EPP in Brood 2	$0 \leq y_2 \leq 1$; $x_2 + y_2 \leq 1$
r_1	Male 1's coefficient of genetic relatedness with his offspring	$0 \leq r_1 \leq 1$
r_2	Male 2's coefficient of genetic relatedness with his offspring	$0 \leq r_2 \leq 1$
r_{121}	Male 1's coefficient of genetic relatedness with Male 2's within-pair offspring	$0 \leq r_{121} \leq 1$
r_{122}	Male 1's coefficient of genetic relatedness with Male 2's extra-pair offspring	$0 \leq r_{122} \leq 1$
r_{21}	Male 2's coefficient of genetic relatedness with Male 1's offspring	$0 \leq r_{21} \leq 1$
b	Male 1's competitive efficiency relative to Male 2	$0 \leq b \leq 1$
v	Male 2's heritable genetic quality relative to Male 1	$0.5 < v < 2$*

Table 2. The relatedness values used to derive predictions specific to the western bluebird population from the tug-of-war model. Values are estimated from those given in Dickinson and Akre (1998).

	Coefficient of relatedness		
Identity of Male 2	r_{121}	r_{122}	r_{21}
Male 1's social father, mated to his mother	0.38	0.38*0.5=0.19	0.38*0.5=0.19
Male 1' stepfather, mated to his mother	0.49*0.49=0.24	0	0
Male 1's brother, mated to an unrelated female	0.38*0.5=0.19	0.38*0.5=0.19	0.38*0.5=0.19
Male 1's social father, mated to an unrelated female	0.38*0.5=0.19	0.38*0.5=0.19	0.38*0.5=0.19

Field methods

We studied the western bluebird population at Hastings Reserve, Carmel Valley, California, which is the subject of a long-term study; details of the population and the monitoring methods are described elsewhere (Dickinson, Koenig, and Pitelka 1996). We conducted male detention trials using methods similar to those previously used in studying western bluebird extra-pair mating behavior (Dickinson 1997; Dickinson 2001). All male detentions we conducted occurred during the laying period, usually after two or three eggs had been laid, when the female was presumably still fertile. Before capturing males for detention, we first conducted a 30-min pre-experimental observation to check that both pair members were alive and on the territory. We captured males using a mount or live decoy in a small cage placed at the base of a mist net close to the nest box. After the male was captured, an assistant removed the male from the mist net, placed him in a cloth bird bag, and immediately left the territory. The assistant took the detained male to the Hastings Reserve aviary, placed him in a large cage, and supplied him with water and

meal worms *ad libitum* for the duration of the 2-hour detention period. Meanwhile, two observers remained on the territory, following the focal female with binoculars and spotting scopes and recording observations using voice recorders. We recorded the identities of all males that intruded onto the focal territory during the detention, and scored the occurrence of extra-pair mating displays (Dickinson, Kraaijeveld, and Smit-Kraaijeveld 2000) and copulation attempts. We defined copulation attempts as attempts by a male to mount a female from behind (Dickinson 1997). We scored copulation attempts as successful when the female remained still and allowed the male to mount her, and as unsuccessful when the female flew or hopped away from the male as he attempted to mount her. After the detained male had been absent from the territory for two hours, an assistant brought him back and released him onto the territory. If an extra-pair male was still present on the territory when the assistant returned with the detained male, we captured the extra-pair male before releasing the detained male. For these captures, we used a mist net with the detained male in a small cage at the base of the net. We conducted all detentions in the morning, beginning the pre-experimental observation before 8:00am, because western bluebird activity peaks during that time; due to the length of the observation period, we were unable to conduct more than one trial per day.

We organized our results into four dyad types: 1) the focal male is the social son of both the second male and his mate, 2) the focal male is the social brother of the second male and is unrelated to the second male's mate, 3) the focal male is the social son of the second male and is unrelated to the second male's mate (his stepmother), 4) the focal male is unrelated to the second male (his stepfather) but is the social son of the second male's mate. Across the three years (2009-2011) of our field study, we identified a total of 60 unique male-year combinations,

comprising 41 unique males, for inclusion in at least one dyad. Some males occurred in more than one dyad type, resulting in a total of 45 dyads for analysis: 12 in which the second pair is father-mother, 9 in which the second pair is brother-unrelated female, 10 in which the second pair is father-stepmother, and 14 in which the second pair is stepfather-mother. Because the length of each trial meant that we could conduct only one trial per day, we could not conduct detention trials at all nests when several pairs laid synchronously. Thus, in 56% (25/45) of dyads we conducted a detention on one of the dyad males but not the other.

Paternity analysis

We selected 37 families for analysis from the western bluebird database, including only nests that had not been subject to any experimental manipulations that could affect natural patterns of paternity. The families occurred in the years 1997 (7), 1998 (10), 1999 (6), and 2007 (14). The 37 families comprised 22 dyads (in which both pairs bred in the same year), in all of which the distance between the two boxes (interbox distance) did not exceed 400 m. In 7 dyads, the second pair consisted of the focal male's social father and mother. In 5 dyads, the second pair consisted of the focal male's social full brother mated to an unrelated female. In 4 dyads, the second pair consisted of the focal male's father mated to an unrelated female (stepmother). In 6 dyads, the second pair consisted of the focal male's mother mated to an unrelated male (stepfather).

We extracted genomic DNA from historical blood samples stored in lysis buffer using QIAGEN DNeasy blood and tissue kits (QIAGEN Inc, Valencia, CA). We used polymerase chain reactions (PCR) to amplify fragments with 13 microsatellite markers previously developed for western bluebirds (Ferree et al. 2008) and used in investigations of western bluebird extra-pair paternity

(Ferree et al. 2010; Ferree and Dickinson 2011). Fragments were sized with an Applied BioSystems 3730xl DNA Analyzer (Life Technologies Corporation, Carlsbad, CA) at Cornell University's Life Sciences Core Laboratories Center. We visually inspected all alleles using GeneMapper 3.7 software (Life Technologies Corporation, Carlsbad, CA). We performed all paternity analyses using the program CERVUS 3.0 (Kalinowski, Taper, and Marshall 2007). For each year, we calculated allele frequencies for the individuals present in that year, and included all adult males for which we had genotypes as candidate fathers. We included social mothers as known parents. We calculated the proportion of sampled candidate fathers by assuming that the total number of adult males recorded on the site in a given year represented 95% of all candidate fathers, and dividing the number of genotyped males by the estimated total number of candidate fathers. The proportion of sampled candidate fathers was low for each year due to the fact that we genotyped selected families from different years rather than all the families in a given year: we estimated the proportion of sampled candidate fathers at 6% (8/138) for 1997, 14% (17/121) for 1998, 11% (9/80) for 1999, and 55% (27/49) for 2007. The proportion is highest for 2007 because we genotyped additional adult males from that year, but not their families, in order to increase our pool of candidate fathers. We specified a typing error rate of 1% to allow for the presence of null alleles at some loci. Across all loci, the combined probability of not excluding a randomly-chosen unrelated male as the genetic sire of an offspring whose mother's identity was known was 1.9×10^{-5} in 1997, 3.8×10^{-6} in 1998, 7.1×10^{-6} in 1999, and 3.1×10^{-6} in 2007.

We assigned genetic sires to 84% (124/147) of nestlings in 92% (34/37) of broods. We only accepted genetic sire assignments when the male was assigned at the 95% confidence interval for the three-way comparison of mother, father, and offspring genotypes. Of the 23 offspring not

assigned a genetic father, 1 had too few successfully genotyped loci for paternity assignment, and 8 had mothers with too few successfully genotyped loci for triadic paternity assignment. These offspring were excluded from further analyses, as they could not be assigned as either within-pair or extra-pair young. The remaining 14 offspring had sufficient genotyped loci for paternity assignment, as did their mothers, but the social father was excluded as the genetic sire; we concluded that these offspring were sired by extra-pair males not included in our samples and classified them as extra-pair young. Extra-pair young occurred in 50% (17/34) of broods with assigned sires, and 21% (24/115) of the young with assigned status (within-pair or extra-pair) were sired by extra-pair males. These rates are similar to those previously found in larger studies of western bluebird extra-pair paternity (Dickinson and Akre 1998; Ferree and Dickinson 2011).

Statistical analysis

We performed all statistical analyses using the program R 2.13.2, using the package lme4 for generalized linear mixed models (R Development Core Team 2011). All means are presented with ± standard error. Because our data were not normally distributed, we used nonparametric tests including Fisher's exact test, the Wilcoxon rank sum test, and the Kruskal-Wallis test. All tests were two-tailed.

We tested whether relative type and distance to the nearest first-order male relative affected the likelihood of intrusion by that relative using a generalized linear mixed model (GLMM) with year and male ID as random effects. Because relative type did not significantly affect distance to the nearest relative of that type (Kruskal-Wallis test: $p>0.05$), we did not include the interaction between relative type and distance as a term in the model. We performed a similar analysis to

examine the effect of relative type and distance to the nearest first-order male relative on the likelihood of that relative gaining a successful copulation with the detained male's mate. In our analysis of whether fathers (mated to either the detained male's mother or to an unrelated female) were more likely to 1) intrude onto the detained male's territory, and 2) having intruded, successfully copulate with the detained male's mate than were stepfathers, we excluded stepfathers that were related to the detained male (e.g., his uncle; 2 cases) or for which we did not conduct a detention of the stepson (7 cases). We used a GLMM with year and male ID as random effects to test whether relative type (father or stepfather), distance to the nearest first-order male relative, or their interaction affected the likelihood of intrusion by that relative. All of our GLMMs employed the binomial error distribution and a logit link because the response variables (intrusions, successful copulations) were binary.

Ethical note

The protocols for capturing, handling, and observing western bluebirds were approved by the Cornell University Institutional Animal Care and Use Committee Protocol (no. 2005-0137) and conducted under permits from the United States Geological Survey Bird Banding Lab (no. 23533), the California Department of Fish and Game (no. 9372), and the United States Fish and Wildlife Service (no. MB20494A-0).

RESULTS

1. Do family members differ in their investments in gaining paternity in a focal male's nest?

A. Model predictions

The model predicts that a male's investment in seeking extra-pair copulations with the focal male's mate is independent of the male's own heritable genetic quality when he is the focal male's stepfather, but varies with his own heritable genetic quality when he is the focal male's father or brother (Figure 5.1). The focal male's father's or brother's investment in seeking EPCs with the focal male's mate is predicted to increase with the father's or brother's own relative heritable genetic quality: related males with higher relative heritable genetic quality invest more in seeking EPCs than related males with lower relative heritable genetic quality. Among males interacting with a son or brother that have heritable genetic quality equal to or greater than the son or brother, males are predicted to invest approximately as much energy in seeking EPCs as males interacting with a stepson. However, males interacting with a son or brother that have heritable genetic quality lower than that relative are predicted to invest less energy in seeking EPCs than males interacting with a stepson. The model makes additional fine-scale predictions but we focus here on the predictions most relevant to our empirical studies.

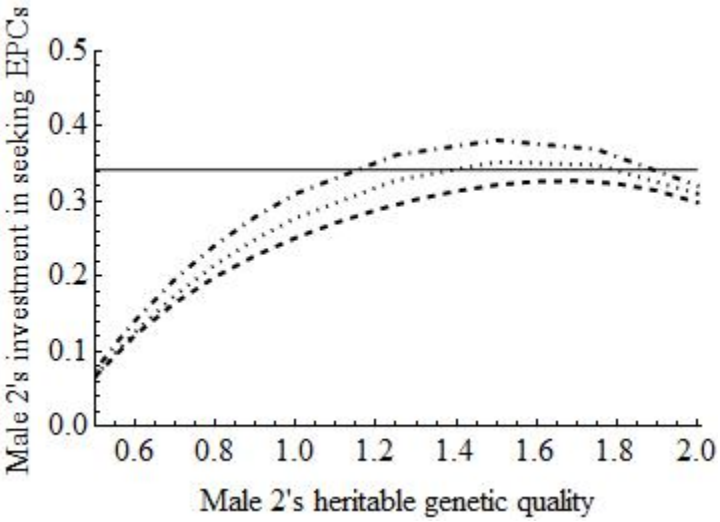

Figure 5.1 The effects of Male 2's heritable genetic quality and relatedness to the focal male on his predicted optimal investment in seeking extra-pair copulations (EPCs) with Male 1's mate. A

stepfather's predicted EPC-seeking investment (solid line) does not vary with his heritable genetic quality. The EPC-seeking investments of fathers breeding in father-mother pairs (dashed line) and fathers breeding in father-stepmother pairs or brothers (dot-dashed and dotted lines) increase with heritable genetic quality. The investments of fathers in father-mother pairs are predicted to be slightly lower than those of male relatives with symmetrical relatedness to the focal male, although investments by symmetrical related males also vary with the relative competitive efficiency of the focal male (equal competitive efficiency, b=1, dot-dashed line; halved competitive efficiency, b=0.5, dotted line).

B. Male detention experiment and genetic paternity analysis results

Male relatives intrude and gain successful copulations during detentions

In 32% (10/31) of the unique (by male-year) trials in which the focal male had a first-order male relative onsite, a male relative intruded onto the detained male's territory during the detention trial. These relatives were the focal male's father (6 cases), brother (1), son (1), half-brother (1), uncle (1), and half-brother/half-uncle (1) (due to related males breeding in different years with the same female, not incestuous mating). The number of cases sums to 11 because during one trial both the detained male's father and his half-brother/half-uncle intruded. In 73% (8/11) of cases the intruding relative gained at least one successful copulation with the detained male's mate. The relatives that gained at least one successful copulation were the detained male's father (5 cases), brother (1), son (1; the copulation was non-incestuous because the father's mate was unrelated to the son), and half-brother (1). The mean number of successful copulations gained by related males was 4.0±1.4, and the mean number of successful copulations gained by first-order related males only was 4.1±1.6.

A first-order male relative only intruded when he was the nearest first-order male relative by interbox distance: the 6 fathers, 1 brother, and 1 son that intruded were each the nearest first-order male relative of the detained male. Additionally, the non-first-order relatives that intruded were breeding in nest boxes either closer than (half-brother, uncle) or nearly as close as (half-brother/half-uncle; 121 versus 116 m) the nearest first-order male relative.

Father were more likely to intrude than sons or brothers

The frequency of intrusions significantly differed among relative types: 55% (6/11) of fathers, 8% (1/12) of sons, and 13% (1/8) of brothers intruded among nearest related neighbors of that relative type (Fisher's exact test: $p=0.0470$) (Figure 5.2). Relative type, but not distance to the nearest relative of that type, affected the likelihood of intrusion by a relative in the detention trial (GLMM: distance, $p=0.0506$; relative type, $p=0.0188$). Different analyses yielded different results with respect to successful copulation likelihood: no relative type was significantly more likely to gain at least one successful copulation with the detained male's mate than the others by Fisher's exact test ($p>0.05$; Table 3), but both relative type and distance to the nearest relative of that type affected the likelihood of successful copulation by a relative in the detention trial by GLMM analysis (distance, $p= 0.0484$; relative type, $p= 0.0326$).

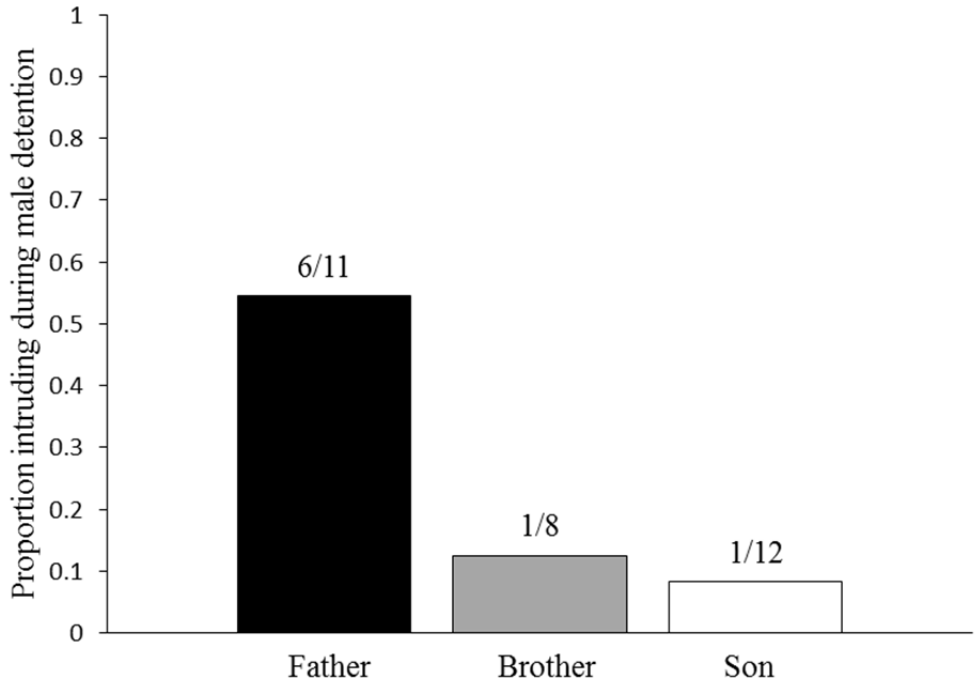

Figure 5.2 The proportion of relatives of each type that intruded when that relative was the nearest first-order male relative to the experimentally detained western bluebird male. Only nearest (by interbox distance) relatives intruded. Fathers were more likely to intrude than brothers or sons (Fisher's exact test: $p=0.0470$).

Table 3. Fisher's exact test results examining the effect of nearest first-order relative type (father, son, or brother) on the likelihood of successful copulation by that relative ($p>0.05$).

Nearest first-order relative	**Copulated successfully**	**Did not copulate successfully**
Father	5	6
Son	1	11
Brother	1	7

Fathers were not more likely than stepfathers to intrude or copulate

Fathers were neither more likely than stepfathers to intrude nor more likely than stepfathers to gain successful copulations (Fisher's exact tests: both, $p>0.05$) (Tables 4 and 5). Neither relative type, distance to the nearest relative of that type, or the interaction between distance and relative type affected the likelihood of intrusion by a father or stepfather in the detention trial (GLMM: all, $p>0.05$).

Table 4. Fisher's exact test results examining the effect of father type (social father or stepfather) on the likelihood of intrusion during the male detention experiment ($p>0.05$).

	Intruded	**Did not intrude**
Father	6	5
Stepfather	0	5

Table 5. Fisher's exact test results examining the effect of father type (social father or stepfather) on the likelihood of successful copulation during the male detention experiment ($p>0.05$).

	Copulated successfully	**Did not copulate successfully**
Father	5	6
Stepfather	0	5

21% of identified extra-pair sires were first-order male relatives of the social father

Among the 34 broods with assigned sires, 50% (17/34) contained at least one extra-pair offspring (EPO). The extra-pair sire was identified for 14 of the 24 EPO, and the identified extra-pair sire

was a relative of the social father in 21% (3/14) of cases. These related extra-pair sires were the social father's father (1), brother (1), and son (1; mating non-incestuously with his stepmother).

Sons were not more likely to lose paternity to fathers than stepfathers

For focal males breeding near either a father and mother or a stepfather and mother, there was no significant difference in the likelihood of losing paternity to a father versus a stepfather (Fisher's exact test: $p>0.05$). The focal male lost paternity to his father in 1/7 (14%) cases and lost paternity to his stepfather in 0/6 (0%) cases.

2. Does breeding near the son of one's mate provide a "paternity buffer" effect?

Fathers did not suffer significantly fewer intrusions or copulations

We observed no instances of stepfathers intruding onto stepsons' territories (0/5 trials), stepsons intruding onto stepfathers' territories (0/10 trials), or sons intruding onto fathers' territories when the father was mated to the son's mother (0/12) during male detentions. We compared the number of intruding males and successful copulation attempts by extra-pair males suffered by fathers versus stepfathers during the male detention trials. Whether we included only intrusions and copulations by unrelated males or by all males, there was no significant difference in either the number of intruding males or the number of successful extra-pair copulation attempts between fathers and stepfathers (Kruskal-Wallis test: both, $p>0.05$)

Fathers retained a significantly higher proportion of within-pair paternity than stepfathers

Interbox distance with fathers (mean=198.4±31.6) was not significantly different from interbox distance with stepfathers (mean=267.6±26.1) (Wilcoxon rank sum test: $p=0.2343$). Father age

and stepfather age were not significantly different (Wilcoxon rank sum test: p=0.3284). Fathers with neighboring sons were not significantly less likely to lose paternity to an extra-pair male (43%; 3/7) than stepfathers with neighboring stepsons (100%; 6/6) (Fisher's exact test: p=0.07). However, fathers with neighboring sons retained a significantly higher proportion of within-pair paternity than did stepfathers with neighboring stepsons (Wilcoxon rank sum test: p=0.0147) (Figure 5.3).

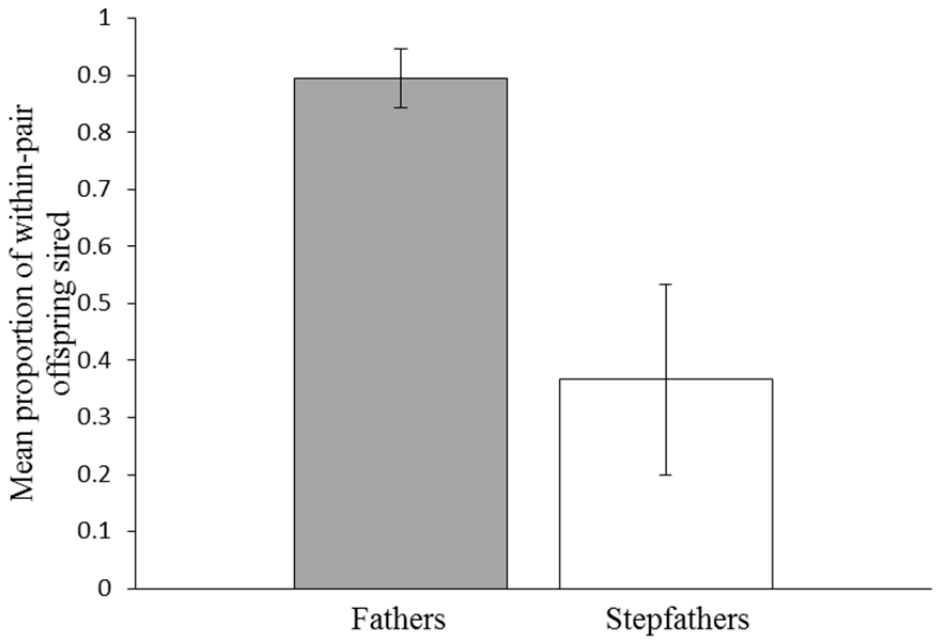

Figure 5.3 The mean proportions of within-pair offspring sired by each western bluebird family member type. Fathers with neighboring sons retained a significantly higher proportion of within-pair paternity than stepfathers with neighboring stepsons (Wilcoxon rank sum test: p=0.0147).

DISCUSSION

Fathers have higher extra-pair copulation-seeking investment than sons or brothers, but not stepfathers

The tug-of-war model (Stern, Dickinson, and Reeve; Chapter 3) as modified here generates predictions specific to western bluebirds regarding the relative amounts of energy males are selected to invest in seeking extra-pair copulations with related males' mates. Importantly, EPC-seeking investment is not primarily moderated by relatedness: depending upon a male's heritable genetic quality, he may be selected to invest more, less, or an equal amount of energy in seeking EPCs with a relative's mate than a non-relative. For a given heritable genetic quality, a father mated to a mother is predicted to invest less in seeking EPCs with his son's mate than is a brother or a father mated to a stepmother, but these differences are small enough that they may be nearly undetectable in field populations. Unfortunately, because the heritable genetic quality curve for western bluebird males is unknown, we cannot explicitly test the model predictions. However, if older individuals have higher heritable genetic quality than young individuals, our finding that fathers are significantly more likely than sons or brothers to intrude onto the detained male's territory would be consistent with the model's predictions, as would our finding that fathers and stepfathers do not differ significantly in likelihood to intrude or copulate with the detained male's mate. Although we found no evidence that a mechanism such as reduced investment in guarding leads to increased extra-pair paternity gained by related males when we compared extra-pair paternity gained by fathers versus stepfathers, the number of broods in which any relative gained paternity was so small that we would be unlikely to detect any existing patterns. Additionally, although fathers, sons, and brothers all gained extra-pair paternity, our

sample size was also too small to detect any differences among relative types in the likelihood of siring offspring in a relative's nest.

Fathers but not stepfathers may enjoy "paternity buffer" benefits when breeding near sons

We were unable to use behavioral data to test the alternative paternity buffer hypotheses because we observed no cases of intrusions by sons onto father-mother pair territories or stepfather-mother pair territories during male detentions, and so were unable to compare their behavior. Our one observation of a son intruding onto his father's territory occurred when the father was mated to a stepmother; during this intrusion, the son copulated with his father's mate. Consistent with the lack of behavioral evidence of mate guarding assistance by sons, we found no difference in the likelihood of suffering intrusions or copulations by extra-pair males among fathers and stepfathers. However, the genetic data provided evidence supporting the son assistance hypothesis for paternity buffering in kin-structured populations. Fathers with neighboring sons retained a significantly higher proportion of within-pair paternity than stepfathers with neighboring stepsons, even though fathers did not breed significantly closer to sons than stepfathers did to stepsons and were not significantly older than stepfathers. The latter is an important point given the known effects of male age on extra-pair mating behavior in western bluebirds (Dickinson 2001; Ferree and Dickinson 2011). Although our sample size is small, this result suggests an interesting potential role for sons in mediating fathers' paternity outcomes, and points towards the importance of modeling triadic interactions among males to fully understand the effects of proximity to kin on male extra-pair mating behavior.

Effects of kin structure on genetic mating system and genetic mating system on kin structure

Our results suggest that both competition and cooperation occur among related western bluebird males in the context of extra-pair mating. Recent research has focused on how the genetic mating system affects selection on kin structure and cooperative behavior, revealing important patterns in the evolutionary trajectories of insects, birds, and mammals (Boomsma 2007; Boomsma 2009; Cornwallis et al. 2010; Lukas and Clutton-Brock 2012). However, an important implication of our results is that kin structure may also affect selection on the genetic mating system. Given the recently-revealed prevalence of kin structure in populations without apparent cooperative behaviors, indicating the potential for "cryptic kin selection" in these populations (Hatchwell 2010), as well as the widespread occurrence of extra-pair mating behavior (Griffith, Owens, and Thuman 2002), studying the potential selection pressure feedbacks between these phenomena is an important goal if we are to understand the evolution of both kin structure and genetic mating systems. Although more data from more species are needed in order to fully understand how extra-pair mating interactions among male relatives may influence population-level patterns of, e.g., extra-pair paternity, our study suggests that examining both behavioral and genetic extra-pair mating patterns in populations with extensive kin structure can lead to greater understanding of the competitive and cooperative interactions among relatives in a context with important fitness consequences.

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